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BREEDING FOR RESISTANCE TO ONION DOWNY MILDEW CAUSED BY PERONOSPORA DESTRUCTOR[1]

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(Results of a coöperative investigation conducted by the United States Department of Agriculture Bureau of Plant Industry and the California Agricultural Experiment Station.)

INTRODUCTION

THE ONION DOWNY-MILDEW FUNGUS, *Peronospora destructor* (Berk.) Casp., is practically world-wide in distribution (*2*, *5*).[5] It was first described in 1841 by Berkeley (*1*) in England, and reported by Trelease (*12*) from Wisconsin in 1884. Subsequently it has been found in a number of other states and has frequently assumed epidemic proportions.

Because adequate control measures have not been developed, the disease continues to cause losses of varying magnitude. Such losses are usually most severe under conditions of moderate temperature and high humidity.

Even though recent work by Yarwood (*14*, *15*) and by McWhorter and Pryor (*7*) indicates the fungicidal efficacy of certain chemical mixtures, the more satisfactory means of prevention involves the development of disease-resistant varieties. In this paper are presented data relative to varietal reaction to mildew, discussion of resistant types that have been found, and the present status of the breeding work designed to transmit resistance to varieties of commercial importance. The studies were made at Davis, California, and at other experimental tracts, as mentioned in the text.

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[5] Italic numbers in parentheses refer to "Literature Cited" at the end of this paper.

PREVALENCE AND DESTRUCTIVENESS IN THE UNITED STATES

Downy mildew, though sporadic in occurrence, is probably the most destructive disease of onions in the United States. It has been abundant at times in each of the principal bulb-producing states, with the exception of Texas, and in each of the seed-producing states with the exception of Idaho. The disease demanded attention in Massachusetts, New York, Michigan, Oregon, and California during the eleven years from 1928 to 1938. The work in the states has been generally focused on host-parasite relations, on factors contributing to or aiding infection, and on fungicidal control. The disease frequently spreads rapidly and ruins large acreages, becoming most prevalent under conditions of high humidity.

On the crops grown for green bunching or for bulbs, downy-mildew infection may significantly reduce the quality and yield of the crop but rarely, if ever, causes complete loss. In New York, Cook (2) reported that bulb enlargement is significantly reduced if the plants become infected when small. In early 1938, at Davis, Sacramento, and Milpitas, in California, many plants of the extremely susceptible varieties Yellow Bermuda and Crystal White Wax were killed by mildew before the bulbs were one-fourth grown. Obviously the injury to the bulb crop is due primarily to killing of the foliage and consequent reduction in the size of the mature bulbs. Although bulbs are occasionally invaded by the mycelium, direct injury from bulb infection does not appear to be serious in America. In crops grown for bulbs or bunching, infected plants may survive and produce a fair crop even after a severe attack on the foliage.

In California the disease is particularly serious in the crop grown for seed. Total loss of seed fields has been observed. Frequently, satisfactory yields are obtained even though the leaves are killed by mildew, but if the seedstalks are severely infected the seed yield is reduced. Mother bulbs are planted from September to January, according to the variety; and, since the seed does not mature until July or August, the foliage is frequently exposed to infection for a period of six months. Normally considerable rainfall, fog, and dew occur from December to April; these conditions combined with favorable temperatures provide ideal conditions for infection, sporulation, and spread of the fungus. As a rule, in the interior valleys conditions become unfavorable for mildew after this time because the humidity decreases and the temperature increases. Along the coast, however, conditions may remain favorable for spread

of mildew considerably longer. Seedstalks usually appear after February 15, the time varying with the variety and date of planting. Obviously, decreases in seed yield are determined by the time and resulting severity of infection. The disease in California, during the last nineteen years, has caused losses as high as 60 to 80 per cent (table 1). In some

TABLE 1

ESTIMATED LOSSES DUE TO DOWNY MILDEW INFECTION OF THE ONION SEED CROP IN CALIFORNIA FROM 1920 TO 1938, INCLUSIVE

Year	Severity	Average loss in seed crop, per cent
1920	Moderately severe, localized; maximum loss 30 per cent	2
1921	Similar to 1920	2
1922	No reports available	..
1923	No reports available	..
1924	No reports available	..
1925	Extremely severe on both seed and bulb crop	60–80
1926	Severe; losses exceeding 50 per cent common in central California and coastal region	40
1927	Moderately severe on seed crop in localized areas	3
1928	Widely distributed on seed crop	5
1929	Little or none in Sacramento Valley; trace in coastal region	0
1930	Severe in localized areas; maximum loss in any area, 75 per cent	25
1931	Severe and general during March; *little spread during April and May but* moderately severe in local areas during June	10
1932	Little infection on seed onions, slight on bulb crop	1
1933	Practically none on seed onions	0
1934	Severe and generally distributed on seed onions	50
1935	Similar to 1934	50
1936	Less than in 1934 and 1935	5
1937	Of little consequence in seed-producing districts	2
1938	Severe in localized districts	8

Source of data:
Observations reported in the *Plant Disease Reporter* for certain years with corresponding volume *and page citations as follows: 1920, 16:237; 1921, 22:354; 1925, 45:68–69 (supplement)*; 1926, 54:279; 1927, 61:261; and 1928, 68:59. All other observations are by the authors.

seasons, the disease became epidemic by March but subsequent environmental conditions were such that only relatively slight infection was evident on seedstalks.

SOURCES OF INOCULUM

Mycelium in Bulbs.—There is abundant evidence that infected onion bulbs harbor the mycelium of the organism, as was first demonstrated by Murphy and McKay (*8*). Plants systemically infected with mildew have been found in seed fields in California, and these are probably the initial sources of inoculum. Additional importance has been given to this method of hibernation by Newhall's observation (*10*) that infected Egyptian or topset onions and potato or multiplier onions serve as im-

portant sources of primary downy-mildew inoculum in the important onion-bulb sections of New York state.

Oöspores in Leaves and Seedstalks.—Oöspores are formed in the tissues of infected plants, but reports in the literature differ as to their abundance. Murphy and McKay in an early paper (*8*) reported that oöspores rarely occurred in fields under their observation but in a later paper (*9*) stated that oöspores are sometimes present in abundance. In central California, large numbers have been found in both infected leaves and seedstalks during several seasons. McKay (*5*) reported germination of oöspores five years old and later (*6*) observed stimulation of germination in 0.01 and 0.02 per cent potassium permanganate.

Infected or Contaminated Seed.—Several investigators have reported infection of flower parts of onion by downy mildew, and Cook (*2*) has demonstrated the presence of mycelium within the ovule. He also found a few oöspores in water used to wash a quantity of commercial seed. Stuart and Newhall (*11*) later reported circumstantial evidence of seed transmission, but no conclusive evidence of the commercial importance of seed transmission has yet been presented.

PRACTICAL DIFFICULTIES IN RELATION TO FUNGICIDAL CONTROL

The fungicidal efficiency of certain chemicals and their toxicity to conidia of many species of the Phycomycetes have been well demonstrated. The literature need not be reviewed here. The problem in connection with onion downy mildew has been to discover chemical mixtures which will adhere to the waxy surfaces of the leaves and seedstalks, particularly during rainy weather. Definite progress has been made in securing such mixtures.

Several factors contribute to the actual inefficiency of these fungicidal materials when applied to the bulb crop of the so-called "intermediate" group of onions. It is the intermediate bulb crop that is most frequently attacked by mildew. On the peat lands, especially, the foliage growth is very rank and does not dry off readily following fog and dew, which provides ideal conditions for infection and sporulation. In California, this crop is usually seeded in the nursery in late August or early September, and the seedlings are transplanted to the field in December and January. On the sedimentary soils, plants are usually set on raised beds spaced about 3 feet from center to center, with seedlings 3 inches apart in the row and two rows to the bed. On peat soils the plants are set on level ground and the rows are spaced about 9 to 10 inches apart. Development aboveground is relatively slow during January and Feb-

ruary but increases thereafter with the rise in temperature. Since growth occurs mainly at the center and base of the plant, new portions of the younger growing leaves are continually becoming exposed to infection. Thus, it is necessary to make frequent applications in order to protect this new growth. This practice, in itself, is almost impossible of execution because the soil is frequently too wet to permit machine applications. Furthermore, while the disease is not epidemic every year, it sometimes appears suddenly and spreads rapidly during favorable weather.

Difficulties are also encountered in spraying the seed crop; frequent spraying is necessary to keep the developing seedstalks covered with fungicide because these, too, grow at the base and continually expose new areas of the stem to infection. Seedstalks, being long and slender, can be completely covered with fungicides only with great difficulty.

The late bulb crop which is usually seeded in the field in January is seldom injured by mildew because the plants make most of their development during the time of year when the air is relatively dry.

LEAF PRUNING AS A CHECK TO SPREAD OF MILDEW

In 1934, mildew appeared very early in some of the small onion-breeding increase plots at Davis. In a plot of the variety strain Stockton G36 (fig. 1, *A*) practically all of the leaves were infected by March 21. A few of the seedstalks had emerged through the surrounding sheaths. It had been observed that where leaf growth was extremely luxuriant, especially following warm, wet winters, mildew was usually much more severe than on sparse foliage; probably this is because the foliage did not dry so quickly after a fog, dew, or rain, or because such leaves may be more susceptible to injury.

In an effort to protect the above-mentioned plot as much as possible against seedstalk infection, all the leaves were trimmed off and the seedstalks left exposed as shown in figure 1, *B*. The seedstalks continued to grow, very little infection occurred, and a good crop of seed was harvested (fig. 1, *C*). While no unpruned plants were left for comparison, the removal of the leaves seemed to have very little deleterious effect on the normal development of the seed crop.

RELATIVE SUSCEPTIBILITY OF VARIETIES

Comparisons of susceptibility were made in 1934 on a number of commercial varieties and foreign introductions planted under overhead irrigation. From one to eight small plots of each lot of the garlic or onion types listed in table 2 were planted in a compact block. On March

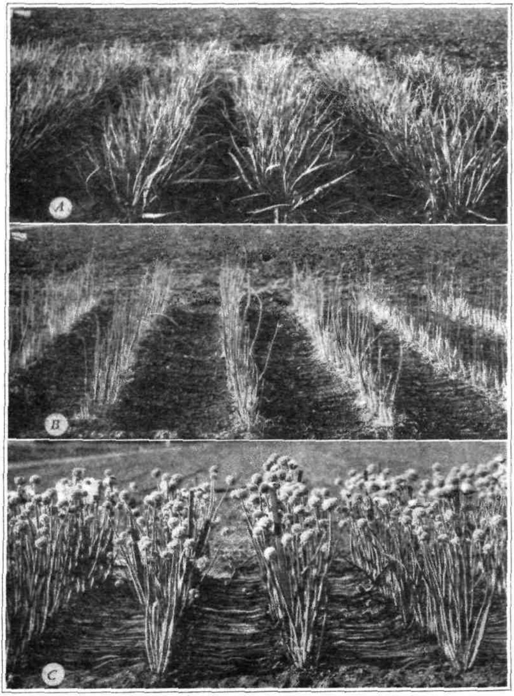

Fig. 1.—*A*, Increase plot of Stockton G36 with luxuriant growth of foliage heavily infected with mildew; photographed March 21, 1934. *B*, The same plot with the mildewed leaves removed to expose the young seed stems; photographed March 22, 1934. *C*, The same plot in full bloom. A normal crop of seed was harvested, indicating that leaf pruning probably did not reduce vigor.

9, and at intervals of a few days thereafter, all plants were sprayed with a suspension of downy-mildew conidia. Humid conditions were maintained by overhead sprinkling. The first sporulation was observed on March 15, and by March 22 infection was abundant and severe on most of the plants. Since in this case the interval (6 days) between inoculation and sporulation was considerably less than that reported by other workers (*2, 13*) under controlled conditions, it appears likely that part of the infection originated from diseased plants previously transplanted into the plot or from wind-borne conidia.

Ratings of the severity of infection on leaves and on seedstalks were made on April 10. The degree of infection was rated from 0 (no infection) to 10 (severe infection), and the results are summarized in table 2. The leaves of all onion varieties showed infection and only commercial Italian Red, Italian Red 13–20–3, and F.P.I. no. 101113 could be considered even moderately resistant. A satisfactory rating of infection on seedstalks could be obtained on only those varieties that produced well-developed seedstalks by April 15, since conditions became unfavorable for uniform infection after that time. Among the varieties forming seed stems early, Italian Red 13–20–3, Early Grano, White Sweet Spanish, and Yellow Strassburg showed the least seedstalk infection; among the most susceptible were Crystal White Wax, Yellow Bermuda, Creole, White Persian, and all of the foreign plant introductions except numbers 101112 and 101113. No infection was observed on garlic.

In the same year an epidemic occurred early in the season on the foliage of the bulb crop of the intermediate varieties such as California Early Red. The leaves of these were badly infected with the exception of Italian Red 13–53, a selection that had been carried along in the breeding plots because of its male sterility. Also the F_1 seedstalks of a cross between Red 21 and 50–6–1, a strain of Stockton Yellow Flat, showed immunity. The foliage and seed stems of all hybrids between *Allium fistulosum* and *Allium cepa* were extremely susceptible (fig. 2).

Another severe downy-mildew epidemic occurred in the breeding plot at Davis in the early months of 1935. Bulbs of certain varieties of the 1934 crop, harvested in July, had been planted in September. The foliage of most plants was badly infected, resulting in premature death of the leaves soon after seedstalk emergence; but the foliage of Italian Red 13–53 again manifested marked resistance. Complete infection was evident on the seedstalks of all varieties and strains except the two Italian Red selections, 13–53 and 13–20–3. Even under the most extreme conditions of infection the seedstalks appeared immune—no lesions were found on them. Many inbred lines and hybrids of susceptible varieties

were killed. In other progenies the primary seedstalks were killed and the secondary stalks were so severely injured that relatively low yields of seed were secured.

TABLE 2

RELATIVE SEVERITY OF DOWNY MILDEW ON THE FOLIAGE AND SEEDSTALKS OF ONION VARIETIES AND GARLIC AT DAVIS IN 1934

Variety or type	Degree of infection*	
	Leaves	Seedstalks
Late garlic	0.0	...
Italian Red 13-20-3	6.3	2.5†
Italian Red (commercial)	5.0	....
Yellow Strassburg	8.3	2.5
Early Grano	10.0	2.5
White Sweet Spanish	8.3	3.0
F. P. I. 101113	5.0	....
F. P. I. 101112	8.3	5.0
Mountain Danvers	10.0	5.0‡
Southport Yellow Globe	7.5	5.0
White Portugal	8.3	5.0
Ohio Yellow Globe	8.3	7.0
Extra Early Red Flat	8.3	6.2
Ebenezer	8.3	6.2
Australian Brown 5-24	10.0	6.2
Yellow Globe Danvers	8.3	7.5
Southport Red Globe	8.3	7.5
Southport White Globe	8.3	7.5
Red Wethersfield	8.3	7.5
Prizetaker	10.0	7.5
Early White Barletta	10.0	7.5
White Persian	7.5	8.3
Creole	10.0	8.3
Yellow Bermuda	10.0	9.2
Crystal White Wax	10.0	10.0
F. P. I. 101171	10.0	10.0
F. P. I. 101224	10.0	10.0
F. P. I. 101460	10.0	10.0
F. P. I. 101461	10.0	10.0
F. P. I. 101499	10.0	10.0
F. P. I. 101515	10.0	10.0

* In the original field data, five degrees of infection were distinguished ranging from 0 (no infection) to 4 (very severe) with plus or minus ratings to identify intermediate groups. To conform to the system of rating used to measure mean injury (table 4) the original ratings were converted to a scale ranging from 0 to 10.

† Although these seedstalks were not examined microscopically, later examination of other seedstalks of this strain showed that similar mildewlike lesions were free from mildew mycelium.

‡ Rating unreliable owing to late formation of seedstalks.

In 1936 several domestic varieties and foreign introductions of *Allium cepa* were grown at Berkeley. White Persian, a thrips-resistant variety recently described by Jones, *et al.* (*3*), was found to be particularly susceptible, many plants being killed by downy mildew before emergence of the seedstalks. Relatively severe infection occurred in leaves and seed-

stalks of Yellow Bermuda, Nebuka, Red Creole, Lord Howe Island, Earliest Express, Giant White Italian Tripoli, Yellow Strassburg, and Southport White Globe. Leaf infection was not noted on Italian Red 13–53. Small mildewlike spots appeared on seedstalks of Italian Red 13–20–3 and were at first thought to indicate downy-mildew infection.

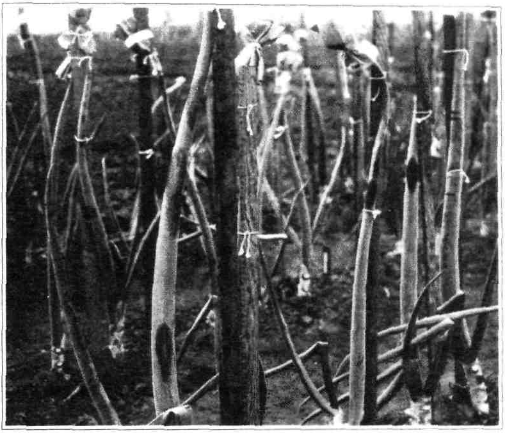

Fig. 2.—Severely infected seedstalks on F_1 plants of Nebuka (*Allium fistulosum* × Australian Brown) in the breeding plot at Davis, California, in March, 1934.

As indicated later, however, the seedstalks of 13–20–3 were immune from infection at Milpitas in 1937 and 1938[6] when 100 per cent infection was noted on many commercial varieties. This apparent discrepancy needs explanation. Small mildewlike lesions frequently occur on seedstalks of 13–53 and 13–20–3 but sporulation has never been observed and microscopic examination of cross sections of such material has never revealed either mycelium or haustoria of the mildew fungus. It is possible that the seedstalk infection charged to 13–20–3 at Berkeley was not actually downy mildew.

[6] Dr. C. E. Yarwood was responsible for the readings made in Berkeley in 1936. He also gave valuable assistance in making the readings at Milpitas in 1937 and 1938.

BREEDING FOR DOWNY-MILDEW RESISTANCE

Three onion strains resistant to downy mildew have been isolated to date. In 1934 the F_1 population (M18) of Red 21 × 50–6–1 produced mildew-free seedstalks. Since Red 21 is susceptible, the resistance of M18 was probably inherited from 50–6–1. The latter strain was an inbred line of Stockton Yellow Flat; and, because seed is no longer available, data on its response to mildew cannot be secured.

The two other resistant strains, numbers 13–53 and 13–20–3, are selections from the variety Italian Red. This variety is of minor importance in California and is seldom grown in other states. Seed is planted in late August, seedlings are transplanted in late November or December, and the plants mature in July in central California. The bulbs are torpedo-shaped, large, red, and mild-flavored. High yields are the rule. The bulbs are poor keepers and for this reason mother bulbs are usually planted in the field in September. Seedstalks of this variety are usually tall and vigorous, producing relatively heavy yields of seed.

Italian Red 13–53.—The Italian Red population from which strain 13–53 was selected was grown at Davis in 1924. In August, a considerable number of desirable bulbs were selected and planted for self-pollination. In April, 1925, the umbels were covered with manila-paper bags when the first flowers opened. The bags were tapped frequently to facilitate self-pollination. These bagged heads were harvested on August 8, and the seed threshed, washed, and dried. From the 5 seed heads of plant 53, 136 bulbils were secured, but no seed. This discovery appeared to have no immediate practical importance, but certainly was of value in a study of sterility. Accordingly, the bulbils were planted and large bulbs were harvested in the summer of 1926. The latter were planted in August, 1926, and another crop of bulbils harvested in July, 1927. In this manner, 13–53 has been asexually propagated since 1925. Bulbil development and type are shown in figures 3 and 4. Interest soon developed in hybrid onions, and 13–53 served as the female parent in a number of crosses (*4*).

Monosmith[7] found that failure of 13–53 to set seed was due to impotent pollen. She found meiosis in the pollen mother cells to be regular but later certain of the tapetal cells degenerated abnormally, with subsequent death of many or all of the microspores. At dehiscence, the pollen-sac contents were cemented together, remaining within the anther.

[7] Monosmith, Helen Ruth. Male sterility in *Allium cepa* L. Unpublished thesis on file at the University of California Library, Berkeley. 1928.

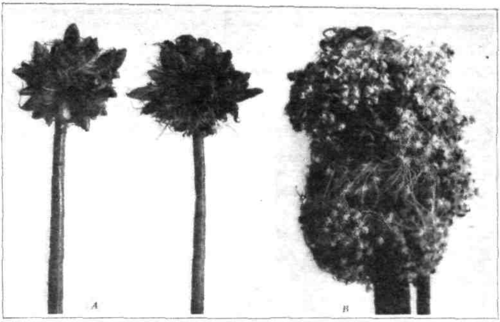

Fig. 3.—*A*, Mature seed heads of Italian Red 13–53 with flower parts removed to show development of bulbils. Although this strain is male-sterile, hybrid seed is readily produced, by using pollen from plants of other varieties. The umbels shown in *B* were bagged with an umbel of an F_1 plant of 13–53 × Red 21. Note the excellent set of seed in the dehisced capsules; also the bulbils in the same head.

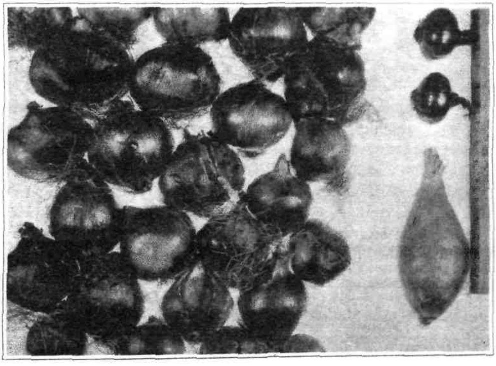

Fig. 4.—At the lower right is a bulb of Italian Red 13–53; at the upper right are bulbs of Lord Howe Island, and at the left is a group of F_1 bulbs involving these two varieties. Note the apparent hybrid vigor of the F_1 hybrid.

The strain is completely male-sterile. During the past twelve years the inflorescences of hundreds of plants of 13–53 have been bagged, but selfed seed has never been found. Fortunately, however, 13–53 forms bulbils, insuring continued asexual propagation.

This selection appears to be the best parent isolated to date for breeding resistant onions. It has a high degree of foliage resistance in field plantings, the amount of injury being negligible even under the most severe epidemic conditions. Infection is usually confined to the tips of the leaves and then grows slowly toward the base. Growth of the fungus in the leaf tissues appears to be exceedingly slow.

Italian Red 13–20–3.—This strain also originated in 1924 as plant 20 of commercial Italian Red. Selfed seed of plant 20 was planted in August, 1925, and plant 3 was selected as a superior bulb in July, 1926. Using bulbs of the 13–20–3 line a California seed company increased the seed supply of this strain in 1929 to replace their own stock of Italian Red. Some of the present Italian Red acreage in California is now 13–20–3. It is similar in type to 13–53 but not male-sterile. This line is well colored and of excellent shape but lacks somewhat in vigor because of inbreeding, and the foliage is not as resistant as that of 13–53.

Since 13–53 and 13–20–3 represent bulbs from the same population of Italian Red, it is evident that there existed in this lot of seed the gene or genes for resistance to downy mildew.

Resistance Tests at Milpitas in 1937.—Because downy-mildew infection at Davis varied significantly from year to year, and because the mildew when it did occur existed in epidemic form only early in the season, it was decided to expose the breeding stocks to infection at Milpitas in the Bay Region, where the disease had been epidemic for several successive years and where conditions most years are favorable for the spread of the disease for a longer time than at Davis. Bulbs were planted at Milpitas during September, 1936, and leaf and seedstalk infection recorded from February to July, 1937. To hasten infection, the first five plants of each strain were artificially inoculated on November 20, 1936, with a conidial suspension from heavily mildewed greenhouse-grown plants. On January 7, 1937, only the inoculated plants showed infection, and, therefore, the remaining population was inoculated at this time. Possibly these artificial inoculations were unnecessary, but because a severe test was essential for evaluating resistance an attempt was made to induce a severe and uniform epidemic. Mildew defoliation of known susceptible types was complete by May 18.

On March 25, when the mean number of leaves to the plant was approximately 35, the total number of leaves and of infected leaves was

determined for each lot. The mean percentage of infected leaves is presented in table 3. Between 74 and 84 per cent of the leaves of Red 21, Stockton G36, Lord Howe Island, and Red Rocco were infected, as compared with only 2 per cent of those of 13–53. As in preceding observations, infection of 13–53 was confined to the tips of the leaves, with no serious interference of the normal leaf functions. Although 30 per cent of all the leaves of 13–20–3 were infected, the injury was not particularly severe. Considerable variation was evident in the amount of leaf infection of the various F_1 hybrids involving 13–53. M23, an F_1 of 13–53 × 13–52–9–6–S_4, manifested only 16 per cent infection, whereas approximately 75 per cent was observed on two F_1 populations of 13–53 × Crystal White Wax. Percentage of infected leaves, however, is not a particularly good measure of resistance, for it does not give a true picture of amount of injury. Most of the leaves might be infected and still the amount of injury be negligible.

The seedstalks of each plant were carefully examined on June 18 and indexed according to an arbitrary rating from 0 to 10 (table 3). The rating of 0 indicated no mildew lesions visible. Microscopic examination of many small mildewlike lesions on strain 13–53 failed to detect the organism. A rating of 10 indicated the most severe degree of infection, usually so weakening the seedstalk that only a very small quantity of seed was matured. Damage was of strictly minor importance until the stage represented by a rating of 4 was reached. From a breeding standpoint, plants rating 1 or 2 are almost as valuable as those which merit rating of 0, and only those plants manifesting stage 4 or higher are considered as suffering from mildew injury.

The seedstalks of 13–53, 13–20–3, M22, M23, and M24 were immune. Actually, mildew did not cause serious damage to any plants of M16, M4, M5, or M17. The nonuniformity of infection of the F_1 hybrids involving 13–53 may be attributed to the fact that neither 13–53 nor several of the commercial varieties had been inbred before making the respective crosses. The reaction of the various F_1 hybrids seems to indicate that resistance is inherited as a dominant character and that the resistant parent is heterozygous for resistance.

The varieties, Stockton G36, Red 21, Red Rocco, and Lord Howe Island were all badly infected. Among 23 plants of Lord Howe Island, two remained free of seedstalk infection; but it is thought that these are escapes rather than an expression of resistance. In most cases the populations were too small to get a good frequency distribution of the different classes of infection.

TABLE 3

Relative Resistance of Onion Varieties, Strains, and Hybrids at Milpitas, in 1937

Pedigree	*Variety or parents*	Generations inbred, or hybrid generations	Leaves infected on March 25, per cent	Number of plants	Distribution of plants among the following eleven classes of seedstalk infection on June 18: 0	1	2	3	4	5	6	7	8	9	10	Mean
13-53	Italian Red (male-sterile)	.	2	26	26	0	0	0	0	0	0	0	0	0	0	0.0
13-20-3	Italian Red	7	30	2	2	0	0	0	0	0	0	0	0	0	0	0.0
M22	13-53×Red Rocco	F_1	47	2	2	0	0	0	0	0	0	0	0	0	0	0.0
M23	13-53×13-52-9-6-8	F_1	16	15	15	0	0	0	0	0	0	0	0	0	0	0.0
M24	13-53×13-20-3	F_1	25	32	32	0	0	0	0	0	0	0	0	0	0	0.0
M16	13-53×Lord Howe Island	F_1	52	24	18	2	2	1	1	0	0	0	0	0	0	0.5
M5	13-53×Stockton G36	F_1	76	8	5	0	2	1	0	0	0	0	0	0	0	0.9
M4	13-53×Crystal White Wax	F_1	74	21	9	5	6	1	0	0	0	0	0	0	0	1.0
M4	13-53×Crystal White Wax	F_1	76	18	9	2	2	2	1	2	0	0	0	0	0	1.4
13-52-9-6-82	Italian Red	5	54	7	4	0	1	0	0	0	0	0	1	0	1	2.9
M17	13-53×Red 21	F_1	53	85	16	20	20	27	2	0	0	0	0	0	0	1.8
M18	50-6-1×Red 21	F_2	58	36	16	4	5	5	3	1	1	0	1	0	0	1.7
MB10	(50-6-1×Red 21)×Red 21	F_1	72	44	4	4	4	6	4	7	9	2	2	1	1	4.2
MB11	(50-6-1×Red 21)×50-6-1	F_1	51	187	1	6	8	32	36	33	24	23	14	9	1	5.0
36-40	Stockton G36	1	83	9	0	0	1	0	3	0	2	0	1	2	0	5.8
21-22-1	Red 21	2	84	40	0	0	1	0	7	11	3	4	9	5	0	6.2
10	Lord Howe Island	.	75	23	2	0	1	2	0	0	2	4	3	4	5	6.9
70	Red Rocco	..	74	2	0	0	0	0	0	0	0	0	0	1	1	9.5

Figure 5 shows the high degree of resistance of both seed stems and foliage of 13–53. Figure 6 shows Crystal White Wax with all leaves killed and all seedstalks very severely injured. These two figures show better than any system of noting the high degree of resistance of 13–53 and the extreme susceptibility of Crystal White Wax.

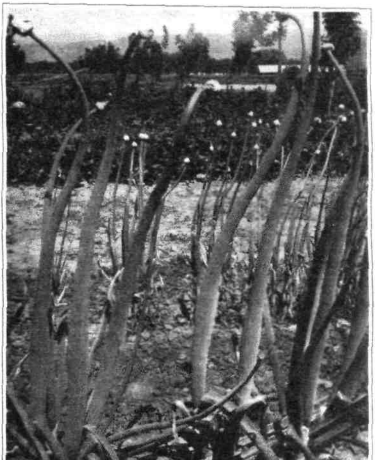

Fig. 5.—Indicating the immunity to downy mildew of seedstalks of Italian Red 13–53 at Milpitas, California, in May, 1937. Note also that the leaves are not severely injured.

Resistance Tests at Milpitas in 1938.—Bulbs for seed production were planted at Milpitas in September, 1937, in the same field where mildew had been so severe that same spring. Many bulbs used had been produced at Milpitas and Sacramento in 1937 and possibly some of these may have also served as sources of infection from perennial mycelium. Weather conditions from December to May were ideal for sporulation and infection. Accordingly, artificial inoculation was unnecessary.

Symptoms were first observed in late December of 1937 and by January 12, 1938, diseased plants were well distributed throughout the plot.

Development of conidia was noted on the foliage on April 6, and these entries appear in table 4 with ratings from 0 to 10, inclusive, as used in other tables. Very striking is the difference in sporulation between Crystal White Wax and the 13–20–3 series as well as that of MB16.

Fig. 6.—Showing extreme susceptibility to mildew of Crystal White Wax at Milpitas, California, in May, 1937. Note the dead leaves and the badly infected seedstalks.

Mother bulbs of 13–53 were not available for inclusion in the seed plot, but seedlings of 13–53 produced by August-planted bulbils were included in the bulb plot at Milpitas. Mildew appeared in this bulb plot in early February. On May 10 and again on June 4 the various populations were rated according to foliage injury. Based on comparative ratings from 0 to 10 on 13–53, foliage injury was only 1 and 2 on the two dates. Lord Howe Island gave readings of 9 to 10 and Crystal White Wax 10 and 10. Strain 13–20–3, however, was only moderately resistant, manifesting stages 4 and 5 injury. Many F_1 populations between susceptible varieties and 13–53 appeared to be about equally resistant, being intermediate between the two parents.

The final readings on injury to the seedstalks, made on July 5, together with the other data are presented in table 4. The sixteen varieties and inbred lines tested may be arranged as follows in the order of decreasing amount of injury: Crystal White Wax, Yellow Bermuda, Yellow Globe Danvers, Early Yellow Globe, Lord Howe Island, Southport

TABLE 4

RELATIVE RESISTANCE OF ONION VARIETIES, STRAINS, AND HYBRIDS AT MILPITAS, IN 1938

Pedigree	Parents or variety	Average degree of sporulation on leaves April 6	Number of plants	Distribution of plants among the following eleven classes of seedstalk infection on July 5: 0	1	2	3	4	5	6	7	8	9	10	Mean
13-20-3	Inbred Italian Red	1.5	28	28	0	0	0	0	0	0	0	0	0	0	0.0
....	Crystal White Wax	8.6	70	0	0	0	0	0	0	0	0	0	0	70	10.0
....	Yellow Bermuda	7.6	50	0	0	0	0	0	0	0	0	0	0	50	10.0
....	Yellow Globe Danvers		10	0	0	0	0	0	0	1	0	1	2	6	9.2
....	Southport Yellow Globe	6.2	10	0	0	0	0	1	0	2	1	0	0	6	8.3
....	Early Yellow Globe	6.6	10	0	0	0	0	0	0	1	0	2	2	5	9.0
....	Lord Howe Island	7.8	49	2	1	0	0	2	1	1	1	1	0	40	8.9
....	Southport White Globe	6.7	10	0	0	0	0	1	0	1	0	2	0	6	8.6
....	White Portugal	7.8	38	0	0	1	0	5	2	2	1	3	3	21	8.1
....	Red Rocco	7.9	22	1	0	1	0	3	1	0	0	1	0	15	8.0
....	Red 21	2.8	36	0	1	1	1	1	4	5	3	5	8	7	7.3
....	Early Grano	4.5	29	2	0	2	0	4	1	2	0	1	0	17	7.4
....	Ebenezer	5.6	33	4	0	5	4	8	2	2	1	1	3	3	4.5
....	Australian Brown	7.1	35	1	0	9	3	3	0	3	0	2	0	14	6.1
....	Sweet Spanish	4.4	37	4	2	6	3	2	2	3	4	1	2	8	5.2
....	Stockton G36	6.7	27	10	0	3	1	1	0	2	0	3	0	7	4.4
M4-1-1	13-53×Crystal White Wax F_2	6.4	43	3	2	2	2	3	1	2	1	3	1	23	7.2
M4-1-2	13-53×Crystal White Wax F_2	7.1	36	3	1	0	1	2	2	2	5	3	0	17	7.3
M4-1-3	13-53×Crystal White Wax F_2	7.2	37	4	0	3	0	2	2	1	1	2	1	21	7.4
M4-1-4	13-53×Crystal White Wax F_2	7.1	39	2	0	1	2	5	1	2	0	3	1	22	7.6
M4-1-5	13-53×Crystal White Wax F_2	6.8	27	3	0	3	0	1	3	1	1	5	0	10	6.6
M4-1-6	13-53×Crystal White Wax F_2	7.3	44	4	1	1	0	0	1	2	0	2	5	28	8.2
M4-1-7	13-53×Crystal White Wax F_2	6.2	49	2	2	2	5	2	5	2	1	3	1	24	7.1
M16-2-1	13-53×Lord Howe Island F_2	3.7	90	52	10	16	5	4	2	1	0	0	0	0	1.0
M16-2-2	13-53×Lord Howe Island F_2	3.8	74	41	14	10	3	5	1	0	0	0	0	0	0.9
M16-2-3	13-53×Lord Howe Island F_2	3.7	78	37	7	4	7	3	8	8	3	1	0	0	2.1
M16-2-4	13-53×Lord Howe Island F_2	2.7	10	3	0	2	2	1	1	1	0	0	0	0	2.5
M16-2-5	13-53×Lord Howe Island F_2	4.7	17	10	0	2	1	0	2	1	1	0	0	0	1.8
M28-1-1	13-53×Red Wethersfield F_2	6.0	6	4	0	0	0	1	0	1	0	0	0	0	1.6
M28-1-2	13-53×Red Wethersfield F_2	6.7	26	24	0	2	0	0	0	0	0	0	0	0	0.2
M28-1-3	13-53×R[illegible] Wethersfield F_2	5.4	15	11	0	0	1	2	1	0	0	0	0	0	1.1
M28-1-4	13-53×[illegible]ethersfield F_2	6.8	20	12	4	1	0	1	1	1	0	0	0	0	1.0
M28-1-5	13-53×[illegible]ethersfield F_2	4.0	90	59	6	10	6	1	1	3	1	2	1	0	1.1
M28-1-6	13-53[illegible]ethersfield F_2	4.7	46	28	3	3	4	3	5	0	0	0	0	0	1.3
MB2	(13-53[illegible]l White Wax)×Crystal White Wax	7.1	30	0	0	0	0	0	1	0	0	2	0	27	9.7
MB12	(13-53[illegible] Grano)×Early Grano	3.4	83	31	5	12	10	2	4	6	2	4	2	5	2.8
MB13	(13-53[illegible]Wethersfield)×Red Wethersfield	5.8	16	10	0	0	2	0	0	0	1	1	1	1	2.5
MB15	(13-53[illegible] Howe Island)×Lord Howe Island	4.5	59	22	4	8	5	8	2	3	1	3	1	2	2.6
MB16	(13-53[illegible])×13-20-3	0.4	17	17	0	0	0	0	0	0	0	0	0	0	0.0

White Globe, Southport Yellow Globe, White Portugal, Red Rocco, Early Grano, Red 21, Australian Brown, Sweet Spanish, Ebenezer, Stockton G36, and Italian Red 13–20–3. Again the 13–20–3 family produced mildew-immune seedstalks, and microscopic examination failed to detect mildew mycelium in the yellowed areas of the seedstalks. Although seedstalks of a few plants of Stockton G36 and other varieties were apparently immune, it is more likely that they escaped infection. The seedstalks of Australian Brown, Ebenezer, and Sweet Spanish emerged much later than those of early and intermediate varieties; this may account for the small amount of damage, since even at Milpitas the conditions become increasingly unfavorable for mildew as the season advances.

All bulbs in the various families of the M4 series were white segregates from the F_2 populations. If there is linkage between color and resistance, then it is possible that all the bulbs selected were susceptible, and that the individuals given a rating of 0—and perhaps those of 1 and 2—were escapes.

Bulbs in families M16–2–1 to M16–2–3 were selected at random from the F_2 population. In families M16–2–4 and M16–2–5, flat bulbs were selected. It is almost impossible to classify the present data into well-defined resistant and susceptible classes, since it is not known if the spots found in the seedstalks of plants in classes 1, 2, and possibly 3, are similar to those found on 13–53 which proved to be free from the mildew fungus. Before the definite mode of inheritance can be determined, the seedstalks of borderline plants will probably need to be examined microscopically to determine definitely in what classes they belong. Also, some means must be established to determine the number of escapes in the apparently immune class. The plants in all of the M16 families were extremely prolific, producing many seedstalks per plant and seed heads of large size. The high degree of immunity and vigor exhibited in these F_3 families indicates the early production of an intermediate variety with resistant foliage and immune seedstalks.

The resistance of the six F_3 families of 13–53 × Red Wethersfield (M28 series) was even more striking than the F_3 of the M16 series; but here again the precautions mentioned above will need to be taken in order to determine definitely the mode of inheritance. It is possible that family M28–1–2 is homozygous-resistant since the two plants in class 2 may actually belong to the immunes. The plants were vigorous and produced a high seed yield.

The data for several backcross progenies, indicated as MB strains, are included in table 4. These backcrosses were made in order to develop

mildew-resistant strains typical of the various varieties. These populations, backcrossed to the susceptible parents, had many plants in the immune and highly resistant classes with the exception of MB2, the backcross to Crystal White Wax.

The Italian Red backcross (13–53 × 13–20–3) × 13–20–3 produced mildew-immune seedstalks. This was to be expected, since those of both parents were immune. Although the foliage of 13–20–3 is usually severely damaged under epidemic conditions, relatively little injury is found on the leaves of 13–53. The degree of sporulation recorded in table 4 is 0.4 which suggests that this population when isolated would be subject to rather light spore inoculation. Probably greater foliage resistance can be incorporated by backcrossing to the 13–53 parent, but by doing this pollen sterility will also be increased. Some one of the progenies from this cross may be the foundation stock for a highly resistant variety which should be adapted to about the same range of conditions as the present Italian Red variety—chiefly those of central California.

SUMMARY

Adequate control measures are still lacking for onion downy mildew, and because the disease frequently appears suddenly in epidemic proportions, heavy losses are often incurred by the bulb and seed grower.

Actual losses incurred by seed growers in California, vary from 0 to 80 per cent, with weather conditions the main conditioning factor. During the past nineteen years, the annual reduction in seed yield has been 10 per cent or higher during six seasons, with a maximum between 60 and 80 per cent in 1925, and several annual losses exceeding 40 per cent.

Certain practical difficulties exist in fungicidal control, making especially desirable the development of resistant varieties.

Three sources of resistance have been found. The most promising is strain 13–53, a male-sterile selection from the Italian Red variety. The seedstalks of this strain are immune and the foliage is highly resistant.

Another strain of Italian Red, designated as 13–20–3, likewise manifests seedstalk immunity but the foliage is only slightly resistant. This latter strain, however, is superior to 13–53 in type.

Seedstalk immunity was also found in the year 1934 in an F_1 hybrid between Red 21 and two inbred lines of Stockton Yellow Flat, namely, 50–6 and 50–6–1.

Measured evidence of varietal and hybrid resistance is indicated in the tables and discussed in the text. Certain F_3 and backcross populations involving 13–53 as the resistant parent are particularly promising.

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A GENETIC ANALYSIS OF RED SEED-COAT COLOR IN PHASEOLUS VULGARIS

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A GENETIC ANALYSIS OF RED SEED-COAT COLOR IN PHASEOLUS VULGARIS[1,2,3]

FRANCIS L. SMITH[4]

INTRODUCTION

SEVERAL VARIETIES *of red beans are grown commercially in California.* The market grades of these beans are determined largely by variations of the red color. The red changes to brownish red and brown after a year or two of storage. The occurrence of brown beans in these red varieties is considered by the trade to indicate old beans. Some varieties, especially Red Kidney, are easily discolored by the sun during the harvest so that occasionally newly threshed beans appear to be a year old.

The present study is a genetic analysis of red seed-coat color in the common bean (*Phaseolus vulgaris* L.) preliminary to a breeding program that might result in the introduction of factors that would stabilize the color of the Red Kidney variety. Commercial conditions are adverse to the introduction of varieties with new colors. The breeding problem, then, resolves itself into making more fast the red color without altering it. The ideal may be visualized as a color between the normal red and a darker red, and it was hoped that such an intermediate type could be developed. Crosses were made between red beans of several varieties. This paper reports the results obtained from these experiments.

REVIEW OF LITERATURE

The common bean is world-wide in distribution and is represented by hundreds of horticultural varieties with scores of seed-coat colors and a number of patterns of distribution of color. The species hybridizes easily. Therefore there is little wonder that the literature on the genetics of this species is voluminous and polylingual. Since different workers used different varieties and described the colors by various standards there is little wonder that the results, too, are variable and often apparently contradictory. There is no standard usage of symbols for the genes which have been analyzed; the same symbol has been used to mean a number of different characters. Beans were used by a number of the

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early hybridists including Mendel (*15*).[5] No attempt will be made here to unravel all the complications and disagreements extant in the literature. This task was undertaken by Kooiman (*7*) in his monograph on the genetics of the genus *Phaseolus*. Reference will be made, however, to earlier workers on those genes encountered in the present studies.

White Color.—Tschermak (*26–29*) was first to report on the white character. In crosses between colored and white beans he assumed a basic factor necessary for color. Later he (*30*) proposed the symbol *A* to represent the presence or absence of this factor. Shull (*22*) used the symbol *P* for yellow or brown pigment and *p* for white; and Emerson (*2, 3*) used the same symbols to represent presence or absence of pigment. In his monograph, Kooiman (*7*) used the *A* symbol to represent the presence of the primary color gene; later workers (*9, 17*) have resorted to the use of *P*. Since the symbol has priority rights this gene will be referred to as *P* in this paper. The conception of *P* is that of a fundamental color gene which of itself gives no color. Thus two types of white beans are possible: *p* whites lacking the fundamental color factor and *P* whites which lack any complementary color genes. This will explain the results of Shaw and Norton (*20*) who obtained colored F_1 plants by crossing two white varieties. Lamprecht (*12*) has obtained *P* white experimentally. Most white varieties, however, are *p* white.

Mottling.—The early workers were greatly concerned with the mottling character. From their results it soon became apparent that there were at least two genetic types of mottling—constant and inconstant.

Some bean varieties are mottled and this is a true breeding character. Tschermak (*28*) showed that mottling was a simple dominant in crosses between mottled and self-colored varieties. He considered the mottling distinct from the color genes. Shull (*22*) designated the symbol *M* for mottled beans and *m* for self-colored. This type of mottling has been studied by a number of workers. Another type of mottling which is similar in breeding behavior was reported by Tjebbes and Kooiman (*25*). The striping factor found in Cranberry beans they thought restricted the expression of the red color to stripes. It was given the symbol *S*. In a later paper Tjebbes (*24*) reported strong linkage between *S*, *B*, and *R*, the latter two being genes for seed-coat color.

Tschermak (*28*), Emerson (*2*), Shull (*21*) and numerous other workers found another type of mottling which was somewhat baffling. Its general characteristics may be seen by the breeding behavior of some crosses. Self-colored × self-colored gave mottled F_1; and F_2 ratio was 1 mottled : 1 self-colored. Self-colored × some white varieties gave mot-

[5] Italic numbers in parentheses refer to "Literature Cited" at the end of this paper.

tled F_1; and in F_2 the ratios were 3 mottled : 3 self-colored : 2 white. Emerson (*2*) called this type of mottling *X*-mottled in contrast to the true-breeding *M* type. Later he (*3*) proposed two closely linked genes *Y* and *Z* as being responsible for both types of mottling. In the mottled varieties both genes were present as dominants *P YZ*. Self-colored races, each with one dominant and one recessive, when crossed would give the inconstant mottled type. For instance, *P yZ* (self-colored) $\times$ *P Yz* (self-colored) would give a mottled F_1, namely $\frac{P\ yZ}{P\ Yz}$. The F_2 from such a cross would segregate into $1\frac{P\ yZ}{P\ yZ}$ (self-colored) : $2\frac{P\ Yz}{P\ yZ}$ (mottled) : $1\frac{P\ Yz}{P\ Yz}$ (self-colored). The genotype *P yz*, he thought, carries no mottling factors. White beans could carry any combination of mottling factors in a latent condition. Since the *yZ* and *Yz* were completely linked, the breeding behavior is the same as expected for a single heterozygous gene. No crossing-over was ever observed between these two hypothetical genes, so their existence could not be proved. Kooiman (*6*) offered a more likely theory of inconstant mottling. A bean with a heterozygous color gene *B* is mottled. When homozygous for *B* the color is darker, and when homozygous for *b* it is lighter. To conserve space homozygous genes will here be represented by a single symbol and heterozygous by the symbols for the dominant and the recessive allelomorphs. The reaction of the *B* gene can be shown in a single case taken from Kooiman's monograph (*7*): *P B C* = coffee brown, *P Bb C* = coffee brown mottled, *P b C* = sallow yellow.

Kristofferson (*8*) used the symbol *K* to represent the same thing: *P K* = black; *P Kk* = black mottled; *P k* = steel gray. This type of mottling has been worked out in great detail by Lamprecht (*9–12*). The color gene which causes mottling when heterozygous he called *C*. It also acts as a modifier in the presence of other color genes. Its action is illustrated in the following zygotic genotypes where mottling is indicated by a slant-line fraction, with the darker color as the numerator and the lighter color as the denominator: *P C J G B* = argus brown; *P Cc J G B* = argus brown/buckthorn brown; and *P c J G B* = buckthorn brown. Likewise, *P C J* = chamois; *P Cc J* = chamois/raw-silk yellow; and *P c J* = raw-silk yellow. And finally, *P C* = sulfur white; *P Cc* = sulfur white/white; and *P c* = white.

In a later paper Lamprecht (*14*) presented data from a cross between Canadian Express and de la Chine. The color of the former was dark plum violet to Bordeaux red; the latter was sulfur white, which was

shown in previous experiments to be *P C j g b v*. The F_1 was weakly mottled, plum violet/chamois. This mottling could not be due to *Cc* because *P C j* is sulfur white and *P c j* is white. He supposed that the heterozygous gene pair *R r* was the cause of mottling. The color reactions observed in F_2 and F_3 were: *P C J R*, dark plum violet; *P C J Rr*, dark plum violet/chamois; *P C J r*, chamois; *P C j R*, light lilac; *P C j Rr*, light lilac/sulfur white; and *P C j r*, sulfur white.

Red Color.—Shaw and Norton (*20*) first called attention to red color inheritance in beans. They recognized two color series, the yellow-black and the red caused by anthocyanins which they represented by *M* and *M′* respectively. Further red modifiers were postulated: *E* for purplish red as in the variety Mohawk, and *D* for light red as in Red Valentine. The supposition of the *M* and *M′* factors seems superfluous in the light of more recent work. Tjebbes and Kooiman (*25*) used three genes to account for the color in Cranberry beans, namely, *R*, *Bl*, and *Z*. Their interactions were represented as follows: *Rr*, pale red; *R*, red; *R*, *Z*, brownish black; *Rr Bl*, violet; *R bl*, purple; *Rr Bl Z*, bluish gray; *R Bl Z*, black. The color due to *r* only was not indicated. Tjebbes (*24*) described wine red as *R c* and Burgundy red as *R C*. The genes *R* and *S* (*S* for striping) were linked with about 1 per cent crossing-over. Reference has already been made to Lamprecht's (*14*) red gene and its phenotypic expression. In some of the crosses reported in the present paper there is segregation for a gene which is similar to Lamprecht's (*14*) *R* because beans heterozygous for this red gene are mottled. Therefore the symbol *R* is used, assuming it is the same gene as Lamprecht's *R*.

Gloyer (*5*) reported progeny tests from a cross, White Kidney × Red Kidney. He made no attempt to analyze the genetics of color, but merely presented his data. Since his data support those obtained in this work they will be summarized later. The red color of Red Kidney behaved as a recessive, the dominant allelomorph being buff. This gene will hereafter be designated as *Rk*.

Eyed Beans.—Emerson (*3*) studied the heredity of partial color in beans. Self-colored × eyed, gave self-colored in the F_1; and in the F_2 they segregated into 3 self-colored : 1 eyed. White × eyed gave self-colored in the F_1, and in the F_2 they segregated into 9 self-colored : 3 eyed : 4 white. He postulated two genes, *P*, the primary pigmentation factor, and *T* a gene which restricted color to the area about the hilum. The interaction was 9 *P T*, self-colored : 3 *P t*, eyed : 4 *p*, white. In addition, he proposed the symbol *E* for self-colored, and *e* for eye pattern. Tschermak (*30*) used the symbol *Z* to represent this pair of genes. Surface (*23*) grew progenies from natural hybrids between New Improved Yellow

Eye (large-eye pattern) and Old Fashioned Yellow Eye (small-eye pattern). The F_1 was piebald, with the color irregularly dispersed over most of the seed. In F_2 he observed 146 piebald : 50 large eye : 70 small eye. He thought the low number in the large-eye class was due to linkage of the pattern factor and a lethal; but his hypothesis was not proved. If the data are fitted to a 2 :1 :1 ratio by χ^2 goodness of fit test, the probability value is .12. The secondary assumption therefore seems ungrounded. The results of Shaw and Norton (*20*) were explained by Emerson's (*3*) *P T* hypothesis. Sax (*19*) believed the eye pattern was due to a double recessive condition for *t* and *e*, because white × eyed gave an F_2 which fitted the ratio of 45 colored : 3 eyed : 16 white better than it did a 9 :3 :4 ratio. Miyaki, *et al.*, (*16*) crossed two partially colored types, saddle × bald, and in F_2 obtained a ratio of 12 bald : 3 saddle : 1 eyed. Lamprecht (*13*) found five genes responsible for twenty-two partial color patterns. These genes were independent of four color genes. In pattern his partial-colored types varied from a dot on either end of the hilum scar to almost complete self color. The dot type was due to the recessive condition of the *bip* (bipunctata) gene; the dominant *Bip* had a "virgarcus" pattern. In the experiments reported in this paper there is but one eye pattern which is similar to Lamprecht's "virgargus" (plate 1, figs. 34, 35). It will be represented by the symbol *E* (self-colored) and *e* (eyed) following Emerson's (*3*) nomenclature.

Colored Hilum Ring.—According to Lamprecht (*12*) three color genes also color the hilum ring in the presence of the ground factor *P*. These are *B*, *J*, and *G*. Prakken (*17*) also noted colored hilum rings with his genes, *S*, *C*, and *V* (probably identical to Lamprecht's *B*). In the studies reported here segregation for hilum ring was found only in some crosses involving the variety Mexican Red which has a black hilum ring.

MATERIALS AND METHODS

The crosses made to provide material for genetic analysis involved varieties of red beans, mottled beans that were predominantly red, white beans, and derivatives from these crosses. In the hybrids it was soon found that some standard of color must be employed to designate the different tints and shades. Ridgway's (*18*) *Color Standards and Color Nomenclature* was used. In order to save time in matching, each time a new color type appeared it was matched with the color book and a specimen sample placed in a Riker mount and labeled with the color name; the beans in each progeny were then matched with the type specimens. These standards represented modal classes, allowing for slight variations. The distinguishable colors are more numerous than the pheno-

types so that the grouping of several closely related colors is necessary to avoid confusion in studying the actual phenotypes. This becomes apparent in F_3 progeny tests made from beans which were classified for color in F_2.

The varieties used in these crosses together with the author's accession numbers were:

Red Kidney 4370 (plate 1, fig. 1)
Red Kidney 4395
Geneva Red Kidney 4387
Nagazura 4390 (plate 1, fig. 2)
Speckled Kidney 50(51)30 (plate 1, fig. 5)
Long Roman 4521 (plate 1, fig. 3)
Red Eye 4387 (plate 1, fig. 34)
White Kidney 4516 (plate 1, fig. 33)
White Kidney of different genotypes derived from F_2 Red Kidney × White Kidney
Dark Red Kidney (65)31 (plate 1, fig. 4)
China Red 4414 (plate 1, fig. 6)
Mexican Red 4437 (plate 1, fig. 8)
Buff (plate 1, fig. 7) derived from true-breeding F_3 extracts of Nagazura × Red Kidney

RESULTS

In this discussion of results the colors of mottled beans are written as a fraction as explained in the section "Review of Literature"; this usage has already been accepted in the literature as indicating mottling. In the tables the zygotic genotypes are represented as follows: heterozygous genes are shown as a fraction, the dominant allelomorph as the numerator and the recessive as the denominator; homozygous genes, either dominant or recessive, are represented by a single symbol. This method makes it easier for the reader to see which genes are segregating. The χ^2 method was used as a measure of goodness of fit. The probability values (P) shown in the tables were taken from Fisher's table for the χ^2 values (*4*). Interpolations of probability were made for χ^2 values which were intermediate between any two values given in the table.

The genetic analysis of the crosses made are discussed in the following paragraphs. Each cross is treated separately and where possible the genotypes of the parents are indicated by symbols in the topic heading.

NAGAZURA × RED KIDNEY

(Formula: *P M Rk bl* × *P m rk Bl*)

Nagazura is a red/buff mottled bean (plate 1, fig. 2). The F_1 was purple/buff (plate 1, figs. 9, 10, 11). It is assumed, therefore, that the Red Kidney (plate 1, fig. 1) carries a gene which changes the red in a mottled bean to purple. This gene is similar in action to the *Bl* described by Tjebbes and Kooiman (*25*) and will therefore be designated by this symbol. In the presence of the recessive *bl*, mottled beans are red-mottled. Since both these varieties are colored, they both carry *P*. Nagazura

carries *M*, the mottling gene. In the F_2 only two self-colored classes were obtained, buff (plate 1, fig. 7) and testaceous, like the Red Kidney (plate 1, fig. 1). Since other red colors will be encountered later, this shade of red will be known as testaceous. This gene pair is represented by *Rk* (buff) *rk* (testaceous). The F_2 should segregate for three genes: *M*, *Rk*, and *Bl*. Since the red parent contributed *Bl* the buff phenotypes may be *P m Rk Bl* or *P m Rk bl* and the testaceous, *P m rk Bl* or *P m rk bl*. In other words, the presence of *Bl* cannot be distinguished in the self-colored segregates. In the mottled beans four classes can be distinguished as follows: *P M Rk Bl* purple/buff, *P M rk Bl* purple/testaceous, *P M Rk bl* red/buff, and *P M rk bl* red/testaceous. Thus, the *Rk* gene can be distinguished in both mottled and self-colored beans, *m Rk* being buff self-colored, *M Rk* mottled on buff background, *m rk* testaceous self-colored, and *M rk* mottled on testaceous background. The *Bl bl* pair can be distinguished only in the mottled types, *M Bl* being purple-mottled and *M bl* red-mottled. The expected ratio in F_2 should be 27 *P M Rk Bl* purple/buff: 9 *P M rk Bl* purple/testaceous: 9 *P M Rk bl* red/buff: 3 *P M rk bl* red/testaceous: 12 *P m Rk* buff: 4 *P m rk* testaceous. F_3 progeny tests were made of a few F_2 phenotypes. The results of F_2 and F_3 from this cross aré presented in table 1.

If the assumptions in respect to the genotypes are correct, the purple/buff (*P M Rk Bl*) should segregate for all three, any two, any one, or none of the genes *M*, *Rk*, *Bl*. In the progenies tested one segregated for *M*, *Rk*, *Bl*; one for *M*, *Bl*; one for *M Rk*; and one for *Bl*.

The purple/testaceous (*P M rk Bl*) should segregate for either one or both of the genes *M* and *Bl*. No purple/buff, red/buff, or buff segregates are expected because all F_2 beans of this phenotype are homozygous for *rk*. Only one progeny test was made. It segregated for *M* and *Bl*. The red/buff (*P M Rk bl*) should segregate for only two genes at most, *M* and *Rk*. No purple mottled are expected in any of the progeny because they all carry *bl*. One of those tested segregated for *M* and *Rk* and another bred true. The buff phenotype (*P m Rk*) should segregate for *Rk* or breed true. Four progeny tests were made; three segregated for *Rk*, the other bred true. The testaceous phenotypes (*P m rk*) should all breed true, and four progeny tests made of this phenotype did so.

SPECKLED KIDNEY × RED KIDNEY

(Formula: *P M Rk bl* × *P m rk Bl*)

The maternal parent of this cross (plate 1, fig. 5) is red/buff. The F_1 was purple/buff (plate 1, fig. 9). The F_2 should segregate 27 *P M Rk Bl* purple/buff: 9 *P M rk Bl* purple/testaceous: 9 *P M Rk bl* red/buff: 3

TABLE 1
NAGAZURA × RED KIDNEY, CROSS No. 30.017
(Formula: $P\ M\ Rk\ bl \times P\ m\ rk\ Bl$)

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Purple/buff ($P\ M\ Rk\ Bl$)	Segregants: Purple/testaceous ($P\ M\ rk\ Bl$)	Segregants: Red/buff ($P\ M\ Rk\ bl$)	Segregants: Red/testaceous ($P\ M\ rk\ bl$)	Segregants: Buff ($P\ m\ Rk$)	Segregants: Testaceous ($P\ m\ rk$)	Segregants: Total	Probability values
F₁ generation				F₂ generation							
Purple/buff	$P\ \frac{M}{m}\ \frac{Rk}{rk}\ \frac{Bl}{bl}$	27:9:9:3:12:4	4	71	33	40	12	39	10	205	0.12
F₂ generation				F₃ generation							
Purple/buff	$P\ \frac{M}{m}\ \frac{Rk}{rk}\ \frac{Bl}{bl}$	27:9:9:3:12:4	1	6	1	2	4	3	0	16	0.01
Purple/buff	$P\ \frac{M}{m}\ Rk\ \frac{Bl}{bl}$	9:0:3:0:4:0	1	15		1	..	2	.	19	0.05
Purple/buff	$P\ M\ Rk\ \frac{Bl}{bl}$	3:0:1:0:0:0	1	8	..	4	..	..		12	0.80
Purple/buff	$P\ \frac{M}{m}\ \frac{Rk}{rk}\ Bl$	9:0:3:0:3:1	1	5	..	1	..	0	2	8	0.10
Purple/testaceous	$P\ \frac{M}{m}\ rk\ \frac{Bl}{bl}$	0:9:0:3:0:4	1	.	7	..	4	..	4	15	0.86
Red/buff	$P\ \frac{M}{m}\ Rk\ bl$	0:0:3:0:1:0	1	..	..	9	..	2	..	11	0.87
Red/buff	$P\ M\ Rk\ bl$	0:0:all	1	..	..	9	..	..	..	9	....
	$P\ m\ \frac{Rk}{rk}$	0:0:0:0:3:1	3	.	..	..	..	64	10	74	0.02

P M rk bl red/testaceous : 12 *P m Rk* buff : 4 *P m rk* testaceous, as did the last cross. Results are shown in table 2. The F_2 with 275 plants gave a probability value of 0.05 fitted to such a ratio. In F_3 the same results should be expected as reported in table 1. Five purple/buff F_3 progenies segregated for *M, Rk*, and *Bl*; one for *M* and *Rk*; three for *M* and *Bl*; three for *Rk* and *Bl*; and three for *Rk*. The purple/testaceous had one progeny segregating for *M* and *Bl*; two for *M*; and three for *Bl*. Two bred true. Three red/buff segregated for *M* and *Rk*, one for *Rk*, and two bred true. Four red/testaceous progenies segregated for *M*. In one of these progenies, there unexpectedly appeared two purple/testaceous plants; these were probably due to natural hybridization with a purple-mottled bean. Three red/testaceous F_2 plants bred true in F_3. Five progenies from buff segregated for *Rk* and six bred true. Eight testaceous progenies bred true as expected.

RED KIDNEY × LONG ROMAN

(Formula: *P m rk Bl* × *P M Rk bl*)

There are two crosses grouped together in table 3. Long Roman (plate 1, fig. 3) is red/buff. The F_1 was purple/buff, so similar results are expected in these crosses as in the preceding ones. The probability value for χ^2 is very small. For this reason the calculated numbers are here given for each color group. The major discrepancy is the low number of purple/testaceous plants and the high number of red/testaceous. The self-colored testaceous class is also low. Is this discrepancy due to some disturbing genetic conditions or could it be due to errors in classification? The three segregating genes are *M, Rk*, and *Bl*. There were 256 mottled (*M*) and 78 self-colored (*m*). This fits a 3:1 ratio with a probability value of 0.49. The total number of beans with *Rk* were 262 and with *rk*, 72. This fits a 3:1 ratio with a probability value of 0.16. Only mottled beans show reaction for the *Bl* gene. There were 168 *Bl* and 88 *bl*. For a 3:1 ratio, 192:64 is expected. The probability value is 0.05. Thus it appears that each gene taken separately fits the expected ratios fairly well.

Linkage between *M* and *Bl* cannot be measured because *Bl* is not apparent in self-colored (*m*) beans. Segregation for *M* and *Rk* was: 196 *M Rk*, 60 *M rk*, 66 *m Rk*, and 12 *m rk*. Fitted to a 9:3:3:1 ratio the expected numbers are 187.87: 62.63: 62.63: 20.87, respectively, with a probability value of 0.22, indicating no linkage. Segregation for *Rk* and *Bl* can be studied only in the mottled beans. The segregation of *Rk* and *Bl* was: 144 *Rk Bl*, 52 *Rk bl*, 24 *rk Bl*, and 36 *rk bl*. For a 9:3:3:1 ratio the calculated numbers for these classes are 144: 48: 48:16. Thus the

TABLE 2

SPECKLED KIDNEY × RED KIDNEY, CROSSES NOS. 30.020 AND 30.021

(Formula: $P\ M\ Rk\ bl \times P\ m\ rk\ Bl$)*

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Purple/buff ($M\ Rk\ Bl$)	Segregants: Purple/testaceous ($M\ rk\ Bl$)	Segregants: Red/buff ($M\ Rk\ bl$)	Segregants: Red/testaceous ($M\ rk\ bl$)	Segregants: Buff ($m\ Rk$)	Segregants: Testaceous ($m\ rk$)	Segregants: Total	Probability values
F₁ generation				**F₂ generation**							
Purple/buff: Cross no. 30.020	$\frac{M}{m}\frac{Rk}{rk}\frac{Bl}{bl}$	27:9:9:3:12:4	1	27	11	11	1	22	5	77	0.23
Cross no. 30.021	$\frac{M}{m}\frac{Rk}{rk}\frac{Bl}{bl}$	27:9:9:3:12:4	4	88	17	37	6	37	13	198	0.13
Total	$\frac{M}{m}\frac{Rk}{rk}\frac{Bl}{bl}$	27:9:9:3:12:4	5	115	28	48	7	59	18	275	0.05
F₂ generation				**F₃ generation**							
Purple/buff	$\frac{M}{m}\frac{Rk}{rk}\frac{Bl}{bl}$	27:9:9:3:12:4	5	78	21	36	11	25	15	186	0.11
	$\frac{M}{m}\frac{Rk}{rk}\ Bl$	9:3:0:0:3:1	1	16	10	..	..	9	1	36	0.28
	$\frac{M}{m}\ Rk\ \frac{Bl}{bl}$	9:0:3:0:4:0	3	71	..	30	..	28	..	129	0.38
	$M\ \frac{Rk}{rk}\frac{Bl}{bl}$	9:3:3:1:0:0	3	69	23	25	3	..	..	120	0.25
	$M\ \frac{Rk}{rk}\ Bl$	3:1:0:0:0:0	3	61	23	..	..	..	..	84	0.63

Purple/testaceous	$\frac{M}{m}\ rk\ \frac{Bl}{bl}$	0:9:0:3:0:4	1	..	13	..	2	..	3	18	0.40
	$\frac{M}{m}\ rk\ Bl$	0:3:0:0:0:1	2	..	43	..	..	..	25	68	0.02
	$M\ rk\ \frac{Bl}{bl}$	0:3:0:1:0:0	3	..	56	..	20	..	..	76	0.79
	$M\ rk\ Bl$	0:all	2	..	61	..	..	..	..	61	....
Red/buff	$\frac{M}{m}\ \frac{Rk}{rk}\ bl$	0:0:9:3:3:1	3	..	..	64	16	26	5	111	0.41
	$M\ \frac{Rk}{rk}\ bl$	0:0:3:1:0:0	5	..	..	104	29	..	..	133	0.70
	$\frac{M}{m}\ Rk\ bl$	0:0:3:0:1:0	1	..	..	20	..	4	..	24	0.36
	$M\ Rk\ bl$	0:0:all	2	..	..	41	..	..	..	41	....
Red/testaceous	$\frac{M}{m}\ rk\ bl$	0:0:0:3:0:1	3	..	..	..	82	..	23	105	0.47
	$\frac{M}{m}\ rk\ bl$	0:0:0:3:0:1	1	..	2†	..	12	..	4	18	....
	$M\ rk\ bl$	0:0:0:all	3	..	..	..	84	..	..	84	....
Buff	$m\ \frac{Rk}{rk}$	0:0:0:0:3:1	5	..	..	..	..	106	30	136	0.44
	$m\ Rk$	0:0:0:0:all	6	..	..	..	..	181	..	181	....
Testaceous	$m\ rk$	0:0:0:0:0:all	8	..	..	..	..	..	233	233	....

* All genotypes in the table are homozygous for *P*.
† Probably field hybrids, with pollen from a purple-mottled bean.

TABLE 3

RED KIDNEY × LONG ROMAN, CROSSES NOS. 33.048 AND 33.052

(Formula: *P m rk Bl* × *P M Rk bl*)*

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Purple/buff (*M Rk Bl*)	Purple/testaceous (*M rk Bl*)	Red/buff (*M Rk bl*)	Red/testaceous (*M rk bl*)	Buff (*m Rk*)	Testaceous (*m rk*)	Total	Probability values
F_1 generation				F_2 generation							
Purple/buff:											
Cross no. 33.048	$\frac{M}{m}\frac{Rk}{rk}\frac{Bl}{bl}$	27:9:9:3:12:4	5	58	11	24	17	27	3	140	Low†
Cross no. 33.052	$\frac{M}{m}\frac{Rk}{rk}\frac{Bl}{bl}$	27:9:9:3:12:4	5	86	13	28	19	39	9	194	Low
Total	$\frac{M}{m}\frac{Rk}{rk}\frac{Bl}{bl}$	27:9:9:3:12:4	10	144	24	52	36	66	12	334	Low
F_2 generation				F_3 generation							
Purple/buff	$\frac{M}{m}\frac{Rk}{rk}\frac{Bl}{bl}$	27:9:9:3:12:4	1	17	8	4	1	4	3	37	0.60

* All genotypes in the table are homozygous for *P*.

† The word "low" is used in those cases where the probability value is less than 0.01.

purple/testaceous (*rk Bl*) class is too small and the red/testaceous (*rk bl*) class is too large for a good fit. The probability value is very low when these data are fitted to such a ratio. Since the *Rk* gene came from one parent, and the *Bl* from the other, the double recessive class *rk bl* should be low if linkage were the cause of the poor fit. As a matter of fact the reason for the poor fit is that this class is too large, which leaves no explanation for the discrepancy except a failure to accurately distinguish between purple/testaceous and red/testaceous color classes.

A single F_2 *purple/buff was tested in* F_3*. Fitted to the expected ratio* for three independently segregating genes these data showed no discrepancy as observed in the F_2, the probability value being 0.60.

RED EYE × RED KIDNEY

(Formula: *P e rk* × *P E rk*)

Red Kidney is testaceous self-colored (plate 1, fig. 1); Red Eye is a white kidney bean with a red eye pattern like Lamprecht's (*13*) "virgarcus" (plate 1, figs. 34, 35).

Now if the red color is genetically the same in both varieties, we should expect a monohybrid segregation for eye pattern, *e*. The F_1 was testaceous self-colored. The F_2 and F_3 ratios are shown in table 4. The probability value for F_2 data fitted to a 3:1 ratio was 0.33 and for nine segregating families in F_3 it was 0.84. Twelve F_3 families from testaceous F_2 were tested; 9 segregated testaceous eye and 3 bred true. The probability value is 0.55 when these data are fitted to the expected 2:1 ratio.

The red color in Red Eye is therefore genetically the same as in Red Kidney. These varieties differ only in the gene *e* for eye pattern. As pointed out by Lamprecht (*13*) this type of pattern may in fact be due to a dominant *Bip* ("virgarcus") gene, the recessive *bip* (bipunctata) not being present. The genotype for Red Kidney then is *P E Bip rk* and for Red Eye *P e Bip rk*.

BUFF × RED EYE, AND RECIPROCAL

(Formulas: *P E Rk* × *P e rk* and *P e rk* × *P E Rk*)

The buff beans used in these reciprocal crosses were true-breeding F_3 extracts from the cross reported in table 1 and were therefore of the genetic constitution *P m Rk*. If the assumptions are true for the cross reported in table 4, the results can be predicted for these. The F_1 should be buff self-colored and the F_2 should segregate into 9 *P E Rk* buff self-colored : 3 *P e Rk* buff eye : 3 *P E rk* testaceous self-colored : 1 *P e rk* testaceous eye. The results are shown in table 5. They are in conformity with expectations. These results prove that the red (testaceous) found

TABLE 4

RED EYE × RED KIDNEY, CROSS NO. 30.018

(Formula: $P\ e\ rk \times P\ E\ rk$)

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Self-colored testaceous ($P\ E\ rk$)	Segregants: Red eye, testaceous ($P\ e\ rk$)	Segregants: Total	Probability values
F₁ generation				F₂ generation			
Self-colored testaceous	$P\ \frac{E}{e}\ rk$	3:1	3	221	64	285	0.33
F₂ generation				F₃ generation			
Self-colored testaceous*	$P\ \frac{E}{e}\ rk$	3:1	9	192	62	254	0.84
	$P\ E\ rk$	all:0	3	92	...	92	....
Red eye (testaceous)	$P\ e\ rk$	0:all	6	...	125	125	....

* There were 9 self-colored families which segregated eyed progenies, and 3 which bred true. The theoretical ratio is 2:1. The probability value when fitted to the theoretical ratio is 0.55.

TABLE 5

BUFF × RED EYE (CROSS NO. 34.162) AND RECIPROCAL (CROSS NO. 34.175)

(Formulas: *P E Rk* × *P e rk* and *P e rk* × *P E Rk*)

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Self-colored buff (*P E Rk*)	Segregants: Self-colored testaceous (*P E rk*)	Segregants: Buff eye (*P e Rk*)	Segregants: Testaceous eye (*P e rk*)	Segregants: Total	Probability values
F_1 generation				F_2 generation					
Buff:									
Cross no. 34.162	$P\frac{E}{e}\frac{Rk}{rk}$	9:3:3:1	14	206	67	75	32	380	0.31
Cross no. 34.175	$P\frac{E}{e}\frac{Rk}{rk}$	9:3:3:1	1	17	4	6	1	28	0.84
Total	$P\frac{E}{e}\frac{Rk}{rk}$	9:3:3:1	15	223	71	81	33	408	0.39

TABLE 9

WHITE KIDNEY × RED KIDNEY, CROSS NO. 30.015

(Formula: $p\ M\ Rk \times P\ m\ rk$)

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Mottled on buff ($P\ M\ Rk$)	Mottled on testaceous ($P\ M\ rk$)	Buff ($P\ m\ Rk$)	Testaceous ($P\ m\ rk$)	White (p)	Total	Probability values
F_1 generation				*F_2 generation*						
Purple/brown	$\frac{P}{p}\frac{M}{m}\frac{Rk}{rk}$	27:9:9:3:16	2	53	20	18	6	36	133	0.99
F_2 generation				*F_3 generation*						
Mottled on buff	$\frac{P}{p}\frac{M}{m}\frac{Rk}{rk}$	27:9:9:3:16	5	83	0	19	9	31	142	Low*
	$\frac{P}{p}\frac{M}{m}Rk$	9:0:3:0:4	2	27	..	10	..	13	50	0.95
	$\frac{P}{p}M\ Rk$	3:0:0:0:1	3	76	..	..	..	22†	98	0.29
	$P\ M\ Rk$	all	3	100	..	..	..	..	100	....
Mottled on testaceous	$\frac{P}{p}\frac{M}{m}rk$	0:9:0:3:4	2	19	0	..	14	5	38	Low
Buff	$\frac{P}{p}m\frac{Rk}{rk}$	0:0:9:3:4	1	..	..	29	7	7‡	43	0.30
	$\frac{P}{p}m\ Rk$	0:0:3:0:1	1	..	..	25	..	10	35	0.64
	$P\ m\frac{Rk}{rk}$	0:0:3:1:0	2	..	..	37	18	..	55	0.19
Testaceous	$P\ m\ rk$	0:0:0:all	1	..	..	..	73	..	73	....
White	p	0:0:0:0:all	4	..	..	..	..	123	123	....

* [illegible] is less than 0.01. † The pistillate parent for cross 34.101. ‡ The pistillate parent for cross 34.160.

in Red Kidney is due to the expression of a recessive gene, the dominant allelomorph being buff, which is represented by the symbol *Rk* (buff) *rk* (testaceous). A recessive gene *e* is responsible for eye pattern demonstrated first by Emerson (*3*). Its dominant allelomorph, *E* makes beans self-colored. There is no indication of linkage between *Rk* and *E*.

WHITE KIDNEY × RED KIDNEY

(Formula: *p M Rk* × *P m rk*)

The F_1 in this cross was mottled purple/buff. The white parent therefore carried *M* and *Rk* and one of the two parents carried *Bl*; it is impossible to know which, because the *Bl* reaction is not evident in either testaceous or white beans. In F_2 there were a number of purple-mottled types ranging from bluish to dark red. These colors were not described accurately enough in the author's original notes to enable one to follow the segregation of *Bl* or its modifiers. The genes segregating in this cross were *P, M,* and *Rk*. The results are shown in table 6. Since all genotypes homozygous for *p* are white, the *M* and *Rk* genes can only be followed in three-fourths of the population. The expected ratio for this cross is 27 *P M Rk* mottled on buff: 9 *P M rk* mottled on testaceous: 9 *P m Rk* buff: 3 *P m rk* testaceous: 16 *p* white. In an F_2 population of 133, a probability value of 0.99 was obtained, when fitted to this ratio. In F_3, five progenies from mottled on buff were segregating for *P, M,* and *Rk*. No mottled-on-testaceous beans were found in a population of 142 although there were 9 self-colored testaceous. The absence of this mottled class made a very poor fit for the expected ratio. Perhaps some mottled-on-testaceous beans were misclassified. Two F_2 mottled-on-buff types segregated for *P* and *M*. Three segregated for *P* and three bred true.

Only two mottled-on-testaceous F_2 plants were submitted to progeny tests. Both segregated for *P* and *M*. The results here are spurious because the mottled offspring were all expected to be mottled on testaceous. There were none of this class but there were 19 mottled on buff which were not expected. This discrepancy may have been due to misclassification of the F_2 plant. The buff F_2 plants could segregate for *P* and *Rk* or breed true. Four were tested in F_3. One segregated for *P* and *Rk;* one for *P;* and one for *Rk*. One testaceous F_2 plant and four whites bred true in F_3.

The results of this cross show segregation for *P, M,* and *Rk*. In F_3 progeny tests, the number of plants mottled on testaceous background (*P M rk*) was usually low. This low number may have been due to misclassification but it is possible that the presence of modifiers altered the segregation of *P M rk* types.

TABLE 7

WHITE KIDNEY × RED KIDNEY, CROSS NO. 32.026

(Formula: *p M Rk bl* × *P m rk Bl*)

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants								Probability values
				Purple/buff (*P M Rk Bl*)	Purple/testaceous (*P M rk Bl*)	Red/buff (*P M Rk bl*)	Red/testaceous (*P M rk bl*)	Buff (*P m Rk*)	Testaceous (*P m rk*)	White (*p*)	Total	
F_1 generation				F_2 generation								
Purple/buff: Heliotrope slate/pinkish buff..........	$\frac{P}{p}\frac{M}{m}\frac{Rk}{rk}\frac{Bl}{bl}$	81:27:27:9:36:12:64	12	218	76	69	19	101	40	165	688	0.71
F_2 generation				F_3 generation								
Testaceous......	*P m rk*	0:0:0:0:0:all	1	...	...	...	...	...	38	...	38	...

WHITE KIDNEY × RED KIDNEY

(Formula: *P M Rk bl* × *P m rk Bl*)

This cross is the same as the one just discussed; the colors in the F_2 were more carefully classified so the segregation of *Bl* could be followed. Table 7 gives a summary of the results. This summary, however, fails to show all the variability encountered. Some phenotype classes contain several colors. The purple/buff class had 54 dark Yvette violet/pinkish buff, 56 Urania blue/pinkish buff, and 108 Ramier blue/pinkish buff, making a total of 218 plants. The purple/testaceous class consisting of 76 plants included 52 analine black/testaceous and 24 dark Corinthian purple/ocher red. The red/buff class had 69 plants which were divided into 19 dark vinaceous-purple/pinkish buff and 50 vinaceous-purple/pinkish buff. The color names indicate that these beans were purple. They showed a slight tinge of purple but were predominantly red. The other colored classes were more uniform, all the red/testaceous were classified as oxblood red/testaceous, all the buff as light pinkish cinnamon, all testaceous as testaceous, and white as white.

There were no F_3 progeny tests made in this cross so it is not possible to say whether the classification made was absolutely correct. Four independent genes were segregated, namely, *P*, *M*, *Rk*, and *Bl*.

GLOYER'S CROSS, WHITE KIDNEY × RED KIDNEY

(Formulas: *p C Rk* × *p c rk* and *P c rk* × *p C Rk*)

In 1928, Gloyer (*5*) reported on a cross between these two varieties. Inasmuch as the *Rk* gene was encountered, his results are given in table 8. He made no attempt to classify the genotypes, so this has been done from his data. The F_1 was mottled brown/buff; it might be supposed, therefore, that White Kidney contributed *M* and *Rk*. In the F_2, however, the segregation was 103 mottled: 102 self-colored: 56 white. This is much nearer a 6:6:4 ratio than to a 9:3:4. The mottling, then, was due to a heterozygous gene like Lamprecht's *C*. The F_1 was brown/buff; and, since brown/buff, brown/red, buff, red, and white were obtained in F_2, this cross obviously segregated for *Rk* as well as for *P* and *C*. In the F_2 a number of brown segregates were found—bronze, brown, dark brown, and seal brown. In F_3 there was no consistency in the way these brown beans segregated. Bronze, for instance, segregated into bronze, brown, and seal brown, but so did seal brown. For purposes of classification the browns may be grouped together. This classification undoubtedly oversimplifies the situation as will appear later. The browns may be considered to be homozygous for *C*. They may be either *P C Rk* or *P C rk*. The

TABLE 8

ANALYSIS OF GLOYER'S CROSS, WHITE KIDNEY × RED KIDNEY AND RECIPROCAL

(Formulas: $p\ C\ Rk \times P\ c\ rk$ and $P\ c\ rk \times p\ C\ Rk$)

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Brown/buff ($P \frac{C}{c} Rk$)	Segregants: Brown/red ($P \frac{C}{c} rk$)	Segregants: Brown ($P\ C\ Rk$ or $P\ C\ rk$)	Segregants: Buff ($P\ c\ Rk$)	Segregants: Red (testaceous) ($P\ c\ rk$)	Segregants: White (p)	Total	Probability values	Natural hybrids: Number	Natural hybrids: Per cent
F₁ generation													
Brown/buff	$\frac{P}{p}\frac{C}{c}\frac{Rk}{rk}$	18:6:12:9:3:16	4	66	37	54	30	18	56	261	0.03	.	...
F₂ generation													
Brown/buff	$\frac{P}{p}\frac{C}{c}\frac{Rk}{rk}$	18:6:12:9:3:16	4	29	14	29	9	3	40	124	0.05	2	1.6
	$\frac{P}{p}\frac{C}{c}Rk$	6:0:3:3:0:4	4	25	..	9	5	.	10	49	0.19	..	...
	$P\frac{C}{c}\frac{Rk}{rk}$	6:2:4:3:1:0	4	44	9	25	17	4	..	99	0.54	10	1.0
	$P\frac{C}{c}Rk$	2:0:1:1:0:0	6	77	..	53	24	..	.	154	0.01	1	0.7
	$P\frac{C}{c}Rk$*	2:0:1:1:0:0	1	22	..	8	12	..	..	42	0.66	..	...
Brown/red	$\frac{P}{p}\frac{C}{c}rk$	0:6:3:0:3:4	6	..	57	33	..	36	46	172	0.68	..	...
	$P\frac{C}{c}rk$	0:2:1:0:1:0	3	..	22	12	..	16	..	50	0.50	..	...

Seal brown..........	$\frac{P}{p}$ *C Rk*	0:0:3:0:0:1	2	..	..	24	..	..	10	34	0.67	..	...
	......†	....	2	..	..	46	12	3	..	62	....	1	1.6
	P C Rk	0:0:all	2	..	..	22	..	..	..	22	....	2	9.1
Bronze.............	$\frac{P}{p}$ *C Rk*	0:0:3:0:0:1	5	..	..	92	..	..	32	124	0.84	1	1.6
	......†	....	1	..	..	41	3	1	10	55	....	..	...
	P C Rk	0:0:all	1	..	..	54	..	..	..	54	....	2	3.7
Buff................	$\frac{P}{p}$ *c* $\frac{Rk}{rk}$	0:0:0:9:3:4	1	..	..	..	12	11	1	24	Low‡	1	4.2
	P c $\frac{Rk}{rk}$	0:0:0:3:1:0	2	..	..	..	50	17	..	67	0.95	2	3.0
	P c $\frac{Rk}{rk}$§	0:0:0:3:1:0	1	..	..	..	29	7	..	36	0.46	1	2.8
	P c Rk	0:0:0:all	3	..	..	..	84	..	..	84	...	3	3.6
Red (testaceous).....	$\frac{P}{p}$ *c rk*	0:0:0:0:3:1	1	..	..	..	..	23	13	36	0.13	..	...
	P c rk	0:0:0:0:all	2	..	..	..	..	67	..	67	....	..	...
White...............	p	0:0:0:0:0:all	12	..	..	..	..	..	491	491	....	3	0.5

* This plant was recorded as buff in F_2 but bred as brown/buff in F_3.
† This type of breeding behavior is not expected on the hypothesis made to explain the results. See discussion in the text.
‡ The word "low" is used in those cases where probability value is less than 0.01.
§ This plant was recorded as brown/buff in F_2 but bred as buff in F_3.

buff and red colors are homozygous for c, buff being P c Rk and red, P c rk. Furthermore, in the mottled beans the brown/buff is *P Cc Rk* and the brown/red *P Cc rk*. Whites, of course, are homozygous for *p*.

Using these assumptions, the F_2 of this cross should segregate as follows: 18 *P Cc Rk* brown/buff : 6 *P Cc rk* brown/red : 12 *P C Rk* and *P C rk* brown : 9 *P c Rk* buff : 3 *P c rk* red : 16 *p* white. The probability value, when the F_2 data on 261 plants were fitted to this theoretical ratio, was 0.03.

Gloyer presented F_3 and F_4 data. In his tables he included plants which were obviously different in color from the major part of the populations. These few cases should be disregarded because they were undoubtedly due to natural hybridization in the field. In a total population of 1,810 F_3 plants, 28 of these off-types were obtained. This would be 1.5 per cent natural cross-pollination. F_4 data need not be considered here because they were presented in such a way that one cannot judge whether the F_4 progenies were from single plants. Some were numerically so large as to preclude such an assumption. The data on F_3 plants are also summarized in table 8. If the assumptions made to explain the F_2 ratios are correct, the F_3 ratios should fall into certain patterns. The mottled types should not breed true but should segregate mottled and self-colored in the ratio of 1:1.

In the brown/buff, segregation for *P, C,* and *Rk* is expected. Four progenies segregated for these three genes. Four progenies also segregated for *P* and *C*. In these cases no red or mottled-on-red beans are expected. Four progenies segregated for *C* and *Rk*. Here no whites are expected. Six progenies segregated for only *C*, giving 1 brown : 2 brown/buff : 1 buff. The fit to this ratio was not very close, the probability value being 0.01. One progeny test of a buff F_2 behaved as a brown/buff segregating for *Cc*. It was probably misclassified in F_2.

F_3 progenies from the brown/red should have segregated for only *P* and *C*. No buff or buff-mottled beans are expected in any of the progenies. Six progenies segregated for *P* and *C* and three for *C* only.

The brown F_2 were grouped into two color classes, seal brown and bronze. If all browns are classed together the breeding behavior is similar in both types. According to the assumptions here proposed by the present author these browns are of the constitution *P C Rk* or *P C rk*. They should segregate for the *P* gene only. As a matter of fact, some buffs and reds appeared in the progeny tests—a result not expected on these assumptions because buffs and reds are both homozygous for *c*. In order to segregate these colors the brown beans would have to be *P Cc Rk rk;* but brown beans cannot be heterozygous for *C*, for these are al-

ways mottled. It is likely, therefore, that these assumptions will have to be amplified to explain the breeding behavior of the brown segregates. Since Gloyer recognized a number of brown colors presumably due to other modifiers this is not fatal to the remainder of the hypothesis.

The buff plants may segregate for *P* and *Rk*. One segregated for both and two for *Rk* only. In addition, one progeny test was made of a brown/buff F_2 which behaved as a buff in F_3, segregating for *Rk*. The red (testaceous) plants should segregate for *P* or breed true. One segregated for *P* and two bred true. The whites, being *p* white, should all breed true and the results of twelve progeny tests agreed with the expectation. However, 3 plants with colored beans were found in 491 white F_3 plants; these were undoubtedly due to natural hybridization.

The assumption of three segregating genes, *P*, *C*, and *Rk* will explain most of the results of this cross. A supplementary hypothesis must be made to explain the breeding behavior of some brown beans. This, however, is beyond the purpose of this review which was made to show that the *Rk* gene has been noted in the literature but the relation between the dominant and recessive allelomorphs was not recognized.

WHITE KIDNEY × NAGAZURA

White segregates taken from F_3 White Kidney × Red Kidney, were used as parents in crosses with Nagazura. The white used as the pistillate parent in cross 34.160 was a segregate in an F_3 population from a buff F_2 (table 6). This buff was segregating for *P* and *Rk*. These whites could be *p m Rk* or *p m rk*. The presence of *Bl* or *bl* could not be told since *Bl* does not modify the color of buff beans. The white used as the pistillate parent in cross 34.161 segregated from a purple/buff F_2 plant (table 6). This white should be *p M Rk Bl* since the F_3 test showed segregation for *P* only. These two whites differed in that one carried *M*, the other *m*. F_2 populations of these crosses showed there were actually four white genotypes: *p m rk Bl*, *p m Rk Bl*, *p M rk Bl*, and *p M Rk Bl*. The results of these genotypes used in crosses with Nagazura (*P M Rk bl*) are shown in tables 9–11.

The third type of segregation was hardly expected because in the F_3 family in which the white parental strain appeared there were no testaceous or testaceous mottled beans, so they were assumed to be *Rk*. Possibly the F_3 population was not large enough to recover the *rk* genotypes. All the whites used were homozygous for *Bl*.

In cross 34.160*a* (formula: *p m rk Bl* × *P M Rk bl*), four genes should segregate. The F_2 data fitted to a 81:27:27:9:36:12:64 ratio gave a probability value of 0.27. The results of F_2 and F_3 are summarized in

TABLE 9

WHITE KIDNEY × NAGAZURA, CROSS NO. 34.160*a*

(Formula: *p m rk Bl* × *P M Rk bl*)

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Purple/buff (*P M Rk Bl*)	Purple/testaceous (*P M rk Bl*)	Red/buff (*P M Rk bl*)	Red/testaceous (*P M rk bl*)	Buff (*P m Rk*)	Testaceous (*P m rk*)	White (*p*)	Total	Probability values
F₁ generation				**F₂ generation**								
Purple/buff: Mars violet/buff........	$\frac{P}{p}\frac{M}{m}\frac{Rk}{rk}\frac{Bl}{bl}$	81:27:27:9:36:12:64	3	43	16	20	3	20	5	22	129	0.27
F₂ generation				**F₃ generation**								
Purple/buff: Madder brown/testaceous*...............	$\frac{P}{p}\frac{M}{m}\frac{Rk}{rk}\frac{Bl}{bl}$	81:27:27:9:36:12:64	1	4	0	3	4	2	0	4	17	Low†
Indian purple/light pinkish cinnamon....	$\frac{P}{p}M\frac{Rk}{rk}\frac{Bl}{bl}$	27:9:9:3:0:0:16	1	13	4	3	3	..	..	7	30	Low (30, 30 bracketed)
Slate purple/pinkish buff..................	$\frac{P}{p}M\frac{Rk}{rk}\frac{Bl}{bl}$	27:9:9:3:0:0:16	3	16	5	3	2	..	..	4	30	
Slate purple/pinkish buff..................	$\frac{P}{p}\frac{M}{m}Rk\frac{Bl}{bl}$	27:0:9:0:12:0:16	1	16	..	4	..	4	..	6	30	Low
Slate purple/pinkish buff..................	$\frac{P}{p}\frac{M}{m}\frac{Rk}{rk}Bl$	27:9:0:0:9:3:16	1	3	1	..	..	0	2	4	10	0.05

Taupe brown/light pinkish cinnamon....	$\frac{P}{p}\ M\ \frac{Rk}{rk}\ Bl$	9:3:0:0:0:0:4	1	8	7	..	..	.	..	6	21	0.28
Slate purple/pinkish buff..................	$\frac{P}{p}\ M\ \frac{Rk}{rk}\ Bl$	9:3:0:0:0:0:4	1	7	2	..	..	..	..	5	14	
Indian purple/light pinkish cinnamon....	$\frac{P}{p}\ M\ Rk\ \frac{Bl}{bl}$	9:0:3:0:0:0:4	1	7	..	2	..	..	..	4	13	0.88
Slate purple/pinkish buff..................	$\frac{P}{p}\ \frac{M}{m}\ Rk\ Bl$	9:0:0:0:3:0:4	1	4	..	..	..	6	..	1	11	Low
Slate purple/pinkish buff..................	$P\ \frac{M}{m}\ \frac{Rk}{rk}\ \frac{Bl}{bl}$	27:9:9:3:12:4:0	5	15	1	9	8	9	3	..	45	Low
Slate purple/pinkish buff..................	$P\ M\ \frac{Rk}{rk}\ \frac{Bl}{bl}$	9:3:3:1:0:0:0	1	21	7	5	2	..	..	..	35	0.92
Slate purple/pinkish buff..................	$P\ \frac{M}{m}\ Rk\ \frac{Bl}{bl}$	9:0:3:0:4:0:0	1	3	..	3	..	1	..	..	7	0.92
Taupe brown/light pinkish cinnamon....	$P\ \frac{M}{m}\ Rk\ \frac{Bl}{bl}$	9:0:3:0:4:0:0	1	8	..	1	..	5	..	..	14	
Taupe brown/light pinkish cinnamon....	$P\ \frac{M}{m}\ \frac{Rk}{rk}\ Bl$	9:3:0:0:3:1:0	1	5	0	..	..	4	1	..	10	0.02
Slate purple/pinkish buff..................	$P\ \frac{M}{m}\ \frac{Rk}{rk}\ Bl$	9:3:0:0:3:1:0	1	2	1	..	..	3	2	..	8	
Taupe brown/light pinkish cinnamon....	$P\ \frac{M}{m}\ Rk\ Bl$	3:0:0:0:1:0:0	1	3	..	.		3	..	.	6	0.17

* The colors marked with an asterisk are not in conformity with the breeding behavior in the progeny tests; they may be due to error in the color classification in the F_2.

† The word "low" is used in those cases where the probability value is less than 0.01.

TABLE 9—(*Continued*)
WHITE KIDNEY × NAGAZURA, CROSS NO. 34.160*a*
(Formula: *p m rk Bl* × *P M Rk bl*)

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Purple/buff ($P\ M\ Rk\ Bl$)	Segregants: Purple/testaceous ($P\ M\ rk\ Bl$)	Segregants: Red/buff ($P\ M\ Rk\ bl$)	Segregants: Red/testaceous ($P\ M\ rk\ bl$)	Segregants: Buff ($P\ m\ Rk$)	Segregants: Testaceous ($P\ m\ rk$)	Segregants: White (p)	Total	Probability values
F_2 generation				F_3 generation								
Purple/testaceous:												
Madder brown/testaceous...............	$\frac{P}{p}\frac{M}{m}\ rk\ \frac{Bl}{bl}$	0:27:0:9:0:12:16	1	..	2	..	1	..	3	3	9 }	0.50
Indian purple/light pinkish cinnamon*...	$\frac{P}{p}\frac{M}{m}\ rk\ \frac{Bl}{bl}$	0:27:0:9:0:12:16	1	..	4	..	3	..	3	3	13 }	
Indian purple/light pinkish cinnamon*...	$\frac{P}{p}\ M\ rk\ \frac{Bl}{bl}$	0:9:0:3:0:0:4	1	..	2	..	6	..	..	2	10	Low
Madder brown/testaceous................	$P\ \frac{M}{m}\ rk\ \frac{Bl}{bl}$	0:9:0:3:0:4:0	1	..	2	..	3	..	3	..	8	0.19
Indian purple/light pinkish cinnamon*...	$P\ M\ rk\ \frac{Bl}{bl}$	0:3:0:1:0:0:0	1	..	4	..	2	..	..	..	6	0.65
Red/buff:												
Deep hellebore red/light pinkish cinnamon....	$\frac{P}{p}\frac{M}{m}\ Rk\ bl$	0:0:9:0:3:0:4	2	..	..	15	..	5	..	7	27 }	0.53
Light red/light pinkish cinnamon.........	$\frac{P}{p}\frac{M}{m}\ Rk\ bl$	0:0:9:0:3:0:4	2	..	..	24	..	9	..	8	41 }	
Oxblood red/light pinkish cinnamon....	$\frac{P}{p}\ M\ \frac{Rk}{rk}\ bl$	0:0:9:3:0:0:4	1	.	..	4	3	..	..	4	11	0.43

Oxblood red/jasper red*	$P\ \frac{M}{m}\ \frac{Rk}{rk}\ bl$	0:0:9:3:3:1:0	1	..	..	4	1	2	0	..	7	0.93
Oxblood red/light *pinkish cinnamon*	$P\ \frac{M}{m}\ \frac{Rk}{rk}\ bl$	0:0:9:3:3:1:0	2	..	..	15	6	3	1	..	25	
Oxblood red/light pinkish cinnamon	$P\ M\ \frac{Rk}{rk}\ bl$	0:0:3:1:0:0:0	1	..	..	10	1	..	..	..	11	0.40
Slate purple*/light pinkish cinnamon	$P\ \frac{M}{m}\ Rk\ bl$	0:0:3:0:1:0:0	1	..	..	7	..	3	..	..	10	0.90
Deep hellebore red/light pinkish cinnamon	$P\ \frac{M}{m}\ Rk\ bl$	0:0:3:0:1:0:0	2	..	..	9	..	2	..	..	11	
Oxblood red/light pinkish cinnamon	$P\ M\ Rk\ bl$	0:0:all	1	..	..	10	..	..	..	..	10	....
Red/testaceous:												
Madder brown/testaceous	$\frac{P}{p}\ \frac{M}{m}\ rk\ bl$	0:0:0:9:0:3:4	3	..	..	..	22	..	14	7	43	0.63
Deep hellebore red/light pinkish cinnamon*	$\frac{P}{p}\ \frac{M}{m}\ rk\ bl$	0:0:0:9:0:3:4	1	..	..	..	4	..	3	2	9	
Oxblood red/jasper red	$\frac{P}{p}\ M\ rk\ bl$	0:0:0:3:0:0:1	4	..	..	.	25	.		10	35	0.98
Madder brown/testaceous	$\frac{P}{p}\ M\ rk\ bl$	0:0:0:3:0:0:1	1	..	..		17	.		3	20	
Madder brown/testaceous	$P\ \frac{M}{m}\ rk\ bl$	0:0:0:3:0:1:0	1	..	..	..	9		3		12	0.99
Madder brown/testaceous	$P\ M\ rk\ bl$	0:0:0:all	1	.	.		5		.		6	...

* The colors marked with an asterisk are not in conformity with the breeding behavior in the progeny tests; they may be due to error in the color classification in the F_2.

† The word "low" is used in those cases where the probability value is less than 0.01.

table 9. There were a number of colors in F_3 which were grouped in the following way: purple/buff included raisin black/pinkish buff (plate 1, fig. 9); Indian purple/pinkish buff (plate 1, fig. 10); and dark heliotrope slate/pinkish buff (plate 1, fig. 11). Purple/testaceous included raisin black/testaceous (plate 1, fig. 12) and Indian purple/testaceous (plate 1, fig. 13). Red/buff included oxblood red/pinkish buff (plate 1, fig. 15), maroon/pinkish buff (plate 1, fig. 14); and deep hellebore red/pinkish buff (plate 1, fig. 16). Red/testaceous included oxblood red/testaceous (plate 1, fig. 22) and maroon/testaceous (plate 1, fig. 17). Buff was classed as pinkish cinnamon (plate 1, fig. 7), testaceous as testaceous (plate 1, fig. 1) and white as white (plate 1, fig. 33).

The F_2 color descriptions in general were similar to those of F_3. In one case madder brown was chosen as the standard color. This was an unfortunate choice because both reddish purple and reds were classed in this group. Had colors been chosen a little farther off this borderline description, the F_3 results would appear more convincing. As it is, some madder-brown mottled beans showed in their breeding behavior to be carrying *Bl* and others were homozygous for *bl*. Progeny tests also showed that *P M Rk* and *P M rk* genotypes were not always clearly distinguishable. Some beans described as mottled on buff bred as mottled on testaceous and vice versa. F_3 progeny tests of the purple/buff phenotype showed that one F_2 plant was segregating for *P*, *M*, *Rk*, and *Bl*. The poor fit is due to the small number of 17 plants, where 256 were needed to recover all genotypes. Four segregated for *P*, *Rk*, and *Bl*. Here a poor fit was obtained because fewer red/buff types appeared than were expected. One segregated for *P*, *M*, and *Bl*; one for *P*, *M*, and *Rk*; two for *P* and *Rk*; one for *P* and *Bl*; one for *P* and *M*; five for *M*, *Rk*, and *Bl*; one for *Rk* and *Bl*; two for *M* and *Bl*; two for *M* and *Rk*; and one for *M*.

Of the purple/testaceous F_2 plants subjected to progeny tests, two segregated for *P*, *M*, and *Bl*; one for *P* and *Bl*; and one for *Bl*. In the F_3 progenies from red/buff four segregated for *P* and *M*; one for *P* and *Rk*; one for *P*, three for *M* and *Rk*; one for *Rk*; three for *M*; and one bred true. Four progenies of red/testaceous segregated for *P* and *M*; five for *P*; one for *M*; and one bred true.

With some exceptions, probably caused by misjudgment of color of F_2 plants, these results bear out the assumption that the white parent was *p m rk Bl*. In some cases the size of the population in F_3 was too small for very good agreement with expectancy.

In the F_1 of cross 34.160*b* (formula: *p m Rk Bl* × *P M Rk bl*), *Rk* was homozygous, so no mottled-on-testaceous or self-colored testaceous beans were expected. Three genes were segregating in F_2, *P*, *M*, and *Bl*,

giving a 27 :9 :12 :16 ratio. The F_2 results fitted to this ratio gave a probability value of 0.13.

The purple/buff F_2 plants were slate-purple/pinkish buff and Indian purple/light pinkish cinnamon (plate 1, fig. 10). Both gave results in conformity with expectation. This phenotype may segregate for *P*, *M*, and *Bl*. Two segregated for *P*, *M*, and *Bl*; three for *P* and *M*; three for *P* and *Bl*; two for *M* and *Bl*; four for *P*; two for *Bl*; two for *M*; and one bred true. The red/buff phenotypes were oxblood red/light pinkish cinnamon (plate 1, fig. 15) and light red/light pinkish cinnamon. This phenotype should segregate for only *P* and *M*. Three progenies segregated for *P* and *M*; four for *M*; and five bred true. These results, as shown in table 10, are all in conformity with the assumption that the white parent was *p m Rk Bl*.

In cross 34.161*a* (formula: *P M rk Bl* × *P M Rk bl*), *M* was homozygous so no self-colored types were expected. The segregating genes were *P*, *Rk*, and *Bl*. The F_2 results from two progenies of this cross were as follows: Purple/buff, 73; purple/testaceous, 12; red/buff, 26; red/testaceous, 8; and white, 26. Fitted to the theoretical ratio of 27 :9 :9 :3 : 16 there should be in a population of 145, 61.2 purple/buff, 20.4 purple/testaceous, 20.4 red/buff, 6.8 red/testaceous, and 36.2 white plants. The probability value for such a fit is 0.07. No F_3 progeny tests were made of this cross.

In cross 34.161*b* (formula: *p M Rk Bl* × *P M Rk bl*), *M* and *Rk* were both homozygous; therefore segregation for only *P* and *Bl* was expected in the hybrid. No self-colored or mottled beans with a testaceous background were expected. The results of this cross are presented in table 11. The F_2 results fitted to a 9 :3 :4 ratio gave a probability value of 0.01, owing to the small number of white beans. However, the results from F_3 fitted the expectations very well. The purple/buff were all slate purple/pinkish buff. Four progenies in F_3 segregated for *P* and *Bl*; two for *P*; four for *Bl*; and one bred true. The red/buff which were classified as oxblood red/light pinkish cinnamon in F_2 should have segregated for *P* or bred true because *M* and *Rk* were homozygous. Two progenies tested in F_3 segregated for *P* and five bred true.

The experiments with the whites of known genotypes bear out the conclusions made in the earlier tests. Mottling is due to the presence of a single gene, *M*; in the presence of its recessive allelomorph *m*, the beans are self-colored. The *Rk* gene can be distinguished in both mottled and self-colored beans. In mottled beans the ground color is buff if *Rk* is present and testaceous if *rk* is present; in self-colored beans *Rk* is buff and *rk* is testaceous. *Bl* may be carried in white, testaceous, and buff

TABLE 10

White Kidney × Nagazura, Cross No. 34.160*b*

(Formula: $p\ m\ Rk\ Bl \times P\ M\ Rk\ bl$)

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Purple/buff ($P\ M\ Rk\ Bl$)	Segregants: Red/buff ($P\ M\ Rk\ bl$)	Segregants: Buff ($P\ m\ Rk$)	Segregants: White (p)	Segregants: Total	Probability values
F₁ generation				**F₂ generation**					
Purple/buff: Mars violet/buff	$\frac{P}{p}\frac{M}{m}Rk\frac{Bl}{bl}$	27:9:12:16	2	33	17	21	15	86	0.13
F₂ generation				**F₃ generation**					
Purple/buff: Slate purple/pinkish buff	$\frac{P}{p}\frac{M}{m}Rk\frac{Bl}{bl}$	27:9:12:16	2	18	7	3	11	39	0.36
Slate purple/pinkish buff	$\frac{P}{p}\frac{M}{m}Rk\ Bl$	9:0:3:4	2	12	..	3	6	21	0.28
Slate purple/pinkish buff	$\frac{P}{p}\frac{M}{m}Rk\ Bl$	9:0:3:4	1	6	..	1	4	11	
Slate purple/pinkish buff	$\frac{P}{p}M\ Rk\frac{Bl}{bl}$	9:3:0:4	2	11	5	..	6	22	0.90
Indian purple/light pinkish cinnamon	$\frac{P}{p}M\ Rk\frac{Bl}{bl}$	9:3:0:4	1	17	3	..	5	25	
Slate purple/pinkish buff	$\frac{P}{p}M\ Rk\ Bl$	3:0:0:1	1	12	..	..	2	14	
Slate purple/light pinkish cinnamon	$\frac{P}{p}M\ Rk\ Bl$	3:0:0:1	2	19	..	..	8	27	0.83

Slate purple/pinkish buff	$P \frac{M}{m} Rk \frac{Bl}{bl}$	9:3:4:0	2	20	3	10	..	33	0.36
Indian purple/light pinkish cinnamon	$P\ M\ Rk \frac{Bl}{bl}$	3:1:0:0	2	17	4	..	..	21	0.54
Slate purple/pinkish buff	$P \frac{M}{m} Rk\ Bl$	3:0:1:0	2	24	..	4	..	28	0.19
Slate purple/pinkish buff	$P\ M\ Rk\ Bl$	All	1	13	..	..	..	13	....
Red/buff:									
Oxblood red/light pinkish cinnamon	$\frac{P}{p} \frac{M}{m} Rk\ bl$	0:9:3:4	2	..	17	8	6	31 }	0.79
Light red/light pinkish cinnamon	$\frac{P}{p} \frac{M}{m} Rk\ bl$	0:9:3:4	1	..	11	2	4	17 }	
Oxblood red/light pinkish cinnamon	$\frac{P}{p} M\ Rk\ bl$	0:3:0:1	2	..	21	..	4	25	0.30
Oxblood red/light pinkish cinnamon	$P \frac{M}{m} Rk\ bl$	0:3:1:0	4	..	25	9	..	34	0.95
Oxblood red/light pinkish cinnamon	$P\ M\ Rk\ bl$	0:all	5	..	32			32	...

TABLE 11
WHITE KIDNEY × NAGAZURA, CROSS NO. 34.161*b*
(Formula: *p M Rk Bl* × *P M Rk bl*)

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Purple/buff (*P M Rk Bl*)	Segregants: Red/buff (*P M Rk bl*)	Segregants: White (*p*)	Segregants: Total	Probability values
F_1 generation				**F_2 generation**				
Purple/buff: Mars violet/buff	$\frac{P}{p}$ *M Rk* $\frac{Bl}{bl}$	9:3:4	4	174	75	60	309	0.01
F_2 generation				**F_3 generation**				
Purple/buff: Slate purple/pinkish buff	$\frac{P}{p}$ *M Rk* $\frac{Bl}{bl}$	9:3:4	4	37	13	13	63	0.26
Slate purple/pinkish buff	$\frac{P}{p}$ *M Rk Bl*	3:0:1	2	13	..	5	18	0.79
Slate purple/pinkish buff	*P M Rk* $\frac{Bl}{bl}$	3:1:0	4	38	11	..	49	0.69
Slate purple/pinkish buff	*P M Rk Bl*	All	1	12	..	..	12	....
Red/buff: Oxblood red/light pinkish cinnamon	$\frac{P}{p}$ *M Rk bl*	0:3:1	2	..	22	4	26	0.26
Oxblood red/light pinkish cinnamon	*P M Rk bl*	0:all	5	..	60	..	60	....

beans with no modification in the expression of color. When *Bl* is added to a red-mottled bean the mottling is changed from red to purple. There is no indication of linkage between *M*, *Bl*, or *Rk*.

RED KIDNEY × CHINA RED, AND RECIPROCAL

(Formulas: *P r rk Bl* × *P R Rk bl* and *P R Rk bl* × *P r rk Bl*)

Since both of these varieties were colored they were homozygous for *P*. The China Red is a dark-red bean (plate 1, fig. 6) which matches very closely Ridgway's (*18*) oxblood red or is even a little darker—Victoria lake. The F_1 plants of these crosses were all mottled. If this mottling were due to a heterozygous color gene the ratio of mottled to self-colored in F_2 should be 1:1; actually it was 134:107. In the F_2 segregants eight color types were obtained. Among these were the familiar buff and testaceous. This cross then, was segregating for *Rk*. The presence of *Rk* explains the two ground colors, buff and testaceous in the mottled beans. The action of *Bl* can also be seen in the mottled beans, some being purple mottled, others red. Two other self-colors were obtained in F_2: purple (plate 1, figs. 23, 24) and oxblood red (plate 1, fig. 25). To account for these, the assumption was made that China Red has a red gene similar to, if not identical with Lamprecht's (*14*) *R* which produces mottling when heterozygous; Red Kidney is homozygous for *r*. Segregation for three genes explained the results if the following assumptions for the genotypes were made: *Rr Rk Bl* is purple/buff; *Rr rk Bl* is purple/testaceous; *Rr Rk bl* is red/buff and *Rr rk bl* is red/testaceous. Purple may be *R Rk Bl* or *R rk Bl;* oxblood red may be *R Rk bl* or *R rk bl;* buff may be *r Rk Bl* or *r Rk bl;* and testaceous, *r rk Bl* or *r rk bl*. The expected ratio should be 18:6:6:2:12:4:12:4, respectively, for the eight colors. These assumptions were tested in progenies from F_2 plants. All mottled F_2 beans should segregate mottled and self-colored in the ratio of 1:1. The colors would depend on the interaction of *Rk* and *Bl*.

The purple/buff F_2 should segregate for *R*, *Rk*, and *Bl*. Since the mottling is due to *Rr*, no mottled types should breed true. It is possible, however, for some to be homozygous for *Rk* or *Bl*. Some F_2 progenies bred in F_3 as purple/buff but the colors noted for the F_2 plants were not purple/buff. These plants are indicated in table 12 by an asterisk following the color which is not in conformity with the breeding behavior.

Seventeen F_2 purple/buff segregated for *R*, *Rk*, and *Bl* in F_3; six segregated for *R* and *Rk;* three for *R* and *Bl;* and four for *R*.

Thirteen F_2 purple/testaceous plants were tested in F_3; since *rk* was present in this genotype segregation for only *R* and *Bl* was expected. Nine segregated for *R* and *Bl* and four for *R*.

TABLE 12

RED KIDNEY × CHINA RED (CROSSES NOS. 34.007 AND 33.051) AND RECIPROCAL (CROSS NO. 34.008)
(Formulas: $P\ r\ rk\ Bl \times P\ R\ Rk\ bl$ and $P\ R\ Rk\ bl \times P\ r\ rk\ Bl$)*

arental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Purple/buff ($\frac{R}{r}$ Rk Bl)	Purple/testaceous ($\frac{R}{r}$ rk Bl)	Red/buff ($\frac{R}{r}$ Rk bl)	Red/testaceous ($\frac{R}{r}$ rk bl)	Purple (R Bl)	Oxblood red (R bl)	Buff (r Rk)	Testaceous (r rk)	Total	Probability values
	F_1 generation			F_2 generation									
le/buff:													
y's maroon/cinmon, cross no. 007	$\frac{R}{r}\frac{Rk}{rk}\frac{Bl}{bl}$	18:6:6:2:12:4:12:4	3	26	14	16	8	20	5	21	6	116	
y's maroon/cinmon, cross no. 008	$\frac{R}{r}\frac{Rk}{rk}\frac{Bl}{bl}$	18:6:6:2:12:4:12:4	4	28	15	7	4	18	8	16	4	100	0.22
ay's maroon/cinmon, cross no. .051	$\frac{R}{r}\frac{Rk}{rk}\frac{Bl}{bl}$	18:6:6:2:12:4:12:4	1	9	2	5	0	1	3	3	2	25	
	F_2 generation			F_3 generation									
ple/buff:													
ay's maroon/cinamon	$\frac{R}{r}\frac{Bk}{rk}\frac{Bl}{bl}$	18:6:6:2:12:4:12:4	9	39	15	15	4	28	9	35	7	141	
ull purplish lack/vinaceous innamon	$\frac{R}{r}\frac{Rk}{rk}\frac{Bl}{bl}$	18:6:6:2:12:4:12:4	1	9	3	1	0	1	1	3	2	20	
Dark Yvette iolet/pinkish innamon	$\frac{R}{r}\frac{Rk}{rk}\frac{Bl}{bl}$	18:6:6:2:12:4:12:4	1	0	0	2	2	2	3	1	0	10	0.56
Dull purplish	R Rk Bl	[illegible]	3	4	3	4	0	6	0	7	3	27	

Hay's maroon/cinnamon	$\frac{R}{r}\frac{Rk}{rk}Bl$	6:2:0:0:4:0:3:1	2	12	4	..	..	7	..	8	0	31		
Dull purplish black/ferruginous†	$\frac{R}{r}\frac{Rk}{rk}Bl$	6:2:0:0:4:0:3:1	2	12	2	..	..	11	..	8	5	38	}	0.11
Hessian brown/ferruginous†	$\frac{R}{r}\frac{Rk}{rk}Bl$	6:2:0:0:4:0:3:1	1	13	0	..	..	4	..	0	5	22		
Raisin black/warm buff	$\frac{R}{r}\frac{Rk}{rk}Bl$	6:2:0:0:4:0:3:1	1	2	0	..	..	3	..	0	1	6		
Hessian brown/ferruginous†	$\frac{R}{r}Rk\frac{Bl}{bl}$	6:0:2:0:3:1:4:0	1	5	..	4	..	4	1	4	..	18		
Oxblood red†/pinkish cinnamon	$\frac{R}{r}Rk\frac{Bl}{bl}$	6:0:2:0:3:1:4:0	1	6	..	2	..	4	1	0	..	13	}	0.49
Raisin black/warm buff	$\frac{R}{r}Rk\frac{Bl}{bl}$	6:0:2:0:3:1:4:0	1	0	..	..	..	3	1	4	..	8		
Hay's maroon/cinnamon	$\frac{R}{r}Rk\,Bl$	2:0:0:0:1:0:1:0	2	10	..	..	..	5	..	9	..	24		
Dull purplish black/vinaceous cinnamon	$\frac{R}{r}Rk\,Bl$	2:0:0:0:1:0:1:0	1	3	..	..	..	0	..	3	..	6	}	0.18
Dull violet black/pinkish cinnamon	$\frac{R}{r}Rk\,Bl$	2:0:0:0:1:0:1:0	1	5	..	..	..	1	..	2	..	8		
Purple/testaceous: Dull purplish black/ferruginous	$\frac{R}{r}rk\frac{Bl}{bl}$	0:6:0:2:3:1:0:4	4	..	22	..	6	13	4	..	13	58		
Victoria lake/testaceous	$\frac{R}{r}rk\frac{Bl}{bl}$	0:6:0:2:3:1:0:4	3	..	19		5	11	3		9	47	}	0.81
Hessian brown/ferruginous	$\frac{R}{r}rk\frac{Bl}{bl}$	0:6:0:2:3:1:0:4	2	..	16		10	10	3		12	51		

TABLE 12—(*Continued*)

RED KIDNEY × CHINA RED (CROSSES NOS. 34.007 AND 33.051) AND RECIPROCAL (CROSS NO. 34.008)
(Formulas: *P r rk Bl* × *P R Rk bl* and *P R Rk bl* × *P r rk Bl*)*

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Purple/buff ($\frac{R}{r}$ *Rk Bl*)	Purple/testaceous ($\frac{R}{r}$ *rk Bl*)	Red/buff ($\frac{R}{r}$ *Rk bl*)	Red/testaceous ($\frac{R}{r}$ *rk bl*)	Purple (*R Bl*)	Oxblood red (*R bl*)	Buff (*r Rk*)	Testaceous (*r rk*)	Total	Probability values
F_1 generation				F_2 generation									
rple/testaceous: —*Continued*													
Hessian brown/ferruginous	$\frac{R}{r}$ *rk Bl*	0:2:0:0:1:0:0:1	3	..	20	..	..	21	..	..	9	50	0.08
Dull purplish black/ferruginous	$\frac{R}{r}$ *rk Bl*	0:2:0:0:1:0:0:1	1	..	5	..	..	1	..	..	2	8	
ed/buff:													
Oxblood red/pinkish cinnamon	$\frac{R}{r}\frac{Rk}{rk}$ *bl*	0:0:6:2:0:4:3:1	3	..	..	21	3	..	4	13	0	41	0.71
Oxblood red/testaceous†	$\frac{R}{r}\frac{Rk}{rk}$ *bl*	0:0:6:2:0:4:3:1	4	..	..	17	11	..	10	6	7	51	
Amaranth purple/pinkish cinnamon	$\frac{R}{r}\frac{Rk}{rk}$ *bl*	0:0:6:2:0:4:3:1	1	..	..	7	1	..	4	3	1	16	
Bordeaux/testaceous†	$\frac{R}{r}\frac{Rk}{rk}$ *bl*	0:0:6:2:0:4:3:1	2	..	..	6	4	..	8	5	0	23	
Amaranth purple/pinkish cinnamon	$\frac{R}{-}$ *Rk bl*	0:0:2:0:0:1:1:0	1	..	..	15	..	..	10	6	..	33	

Red/testaceous:													
Oxblood red/testaceous	$\frac{R}{r}$ *rk bl*	0:0:0:2:0:1:0:1	6	..	..	..	41	..	25	..	24	90	0.87
Bordeaux/testaceous	$\frac{R}{r}$ *rk bl*	0:0:0:2:0:1:0:1	1	..	..	..	3	..	0	..	0	3	
Purple:													
Dull purplish black	$R\ \frac{Bl}{bl}$	0:0:0:0:3:1:0:0	10	..	..	..	..	129	46	..	..	175	
Raisin black	$R\ \frac{Bl}{bl}$	0:0:0:0:3:1:0:0	1	..	..	..	..	15	1	..	..	16	0.70
Liver brown	$R\ \frac{Bl}{bl}$	0:0:0:0:3:1:0:0	2	..	..	..	..	25	6	..	..	31	
Dull purplish black	*R Bl*	0:0:0:0:all	4	..	..	..	..	82	..	..	..	82	....
Liver brown	*R Bl*	0:0:0:0:all	1	..	..	..	..	11	..	..	..	11	....
Oxblood red:													
Oxblood red	*R bl*	0:0:0:0:0:all	4	..	..	..	..	..	61	..	..	61	....
Pompeian red	*R bl*	0:0:0:0:0:all	8	..	..	..	..	..	151	..	..	151	....
Bordeaux	*R bl*	0:0:0:0:0:all	1	..	..	..	..	..	4	..	..	4	....
Buff:													
Vinaceous cinnamon	$r\ \frac{Rk}{rk}$	0:0:0:0:0:0:3:1	3	..	..	..	..	..	..	38	15	53	0.99
Light pinkish cinnamon	$r\ \frac{Rk}{rk}$	0:0:0:0:0:0:3:1	2	..	..	..	..	..	..	22	5	27	
Vinaceous cinnamon	*r Rk*	0:0:0:0:0:0:all	2	..	..	..	..	..	..	32	..	32	....
Testaceous	*r rk*	0:0:0:0:0:0:0:all	2	..	..	..	..	..	..	..	18	18	....

* All genotypes in the table are homozygous for *P*.

† The colors marked with a dagger are not in conformity with the breeding behavior in the progeny tests; they may be due to error in the color classification in the F_2.

Seventeen F_2 red/buff were tested in F_3. Some of these had been misclassified as red/testaceous in F_2. Since red/buff is *Rr Rk bl* segregation for only *R* and *Rk* is possible. Ten progenies segregated for *R* and *Rk*, and seven for *R*.

Seven red/testaceous F_2 plants were tested in F_3. This genotype, being *Rr rk bl*, should segregate for *R* only, giving 1 *R rk bl* oxblood red : 2 *Rr rk bl* red/testaceous : 1 *r rk bl* testaceous. The numbers obtained were 25 :44 :24. If the assumptions made were correct, the purple F_2 should segregate for *Bl* only. Thirteen progenies segregated for *Bl* and five bred true. All oxblood red phenotypes should breed true. The thirteen tested conformed to expectation. The buff phenotypes should segregate for *Rk* or breed true. Five segregated for *Rk* and two bred true. Only two testaceous F_2 were grown in F_3 and they bred true as expected.

CHINA RED × RED KIDNEY

(Formula: *P R rk bl* × *P r rk Bl*)

In this cross the F_1 was purple/testaceous rather than purple/buff as in the crosses reported in table 12. The China Red in this cross must have been *P R rk bl* while in the others it was *P R Rk bl*. The F_2 was in conformity with expectations in that no buff or mottled-on-buff beans appeared. The F_3 progenies grown from F_2 plants were all homozygous for *rk*. Seventeen purple/testaceous F_2 plants were tested in F_3. Eight of them segregated for *R* and *Bl* and nine segregated for *R* only. Seven red/testaceous segregated for *R* as expected. Five purple F_2 segregated in F_3 for *Bl* and three bred true. One oxblood red bred true as did three testaceous.

The color of China Red, then, is due to the presence of *R*. This variety may carry *Rk* (table 12) or *rk* (table 13). In all crosses there was segregation for the purple gene *Bl*, the dominant allelomorph coming from Red Kidney. Only one strain of China Red has been used in the crosses but the results found here prove that within the variety there are at least two genotypes. Since the presence of *Rk* does not alter the color of the bean, this genetic variation in the variety cannot be detected by examination of the beans themselves.

CHINA RED × GENEVA RED KIDNEY

The F_1 and F_2 data from this cross are given in table 14. The Geneva Red Kidney is a testaceous segregate from the cross White Kidney × Red Kidney made by Gloyer (*5*). A summary of his results regarding color segregation was given in table 8. Owing to its origin, this variety may carry brown modifiers, at least *c*, and probably others which could

TABLE 13

CHINA RED × RED KIDNEY, CROSS NO. 34.173

(Formula: $P\ R\ rk\ bl \times P\ r\ rk\ Bl$)*

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Purple/testaceous $(\frac{R}{r}\ rk\ Bl)$	Red/testaceous $(\frac{R}{r}\ rk\ bl)$	Purple $(R\ Bl)$	Oxblood red $(R\ bl)$	Testaceous $(r\ rk)$	Total	Probability values
F₁ generation				**F₂ generation**						
Purple/testaceous: Victoria lake/testaceous....	$\frac{R}{r}\ rk\ \frac{Bl}{bl}$	6:2:3:1:4	2	35	14	10	4	28	91	0.23
F₂ generation				**F₃ generation**						
Purple/testaceous: Victoria lake/testaceous....	$\frac{R}{r}\ rk\ \frac{Bl}{bl}$	6:2:3:1:4	8	23	11	17	4	9	64	0.12
Victoria lake/testaceous....	$\frac{R}{r}\ rk\ Bl$	6:0:1:0:1	9	53	..	31	..	20	104	0.81
Red/testaceous: Oxblood red/testaceous....	$\frac{R}{r}\ rk\ bl$	0:2:0:1:1	7	..	51	..	32	22	105	0.38
Purple: Victoria lake..............	$R\ rk\ \frac{Bl}{bl}$	0:0:3:1:0	5	..	..	56	21	..	77	0.86
Victoria lake..............	$R\ rk\ Bl$	0:0:all	3	..	..	49	..	.	49	....
Oxblood red..............	$R\ rk\ bl$	0:0:0:all	1	..	.		4		4	...
Testaceous..............	$r\ rk$	0:0:0:0:all	3			.	...	34	34	...

* All genotypes in the table are homozygous for P.

TABLE 14

CHINA RED × GENEVA RED KIDNEY, CROSS No. 34.177

Parental colors	Progenies tested	Segregants: Black	Liver brown	Corinthian purple	Chestnut brown	Mahogany red	Hay's russet	Deep Corinthian red	Carmine	Oxblood red	Vinaceous fawn	Testaceous	Total
F_1 generation		F_2 generation											
Liver brown	7	..	33	4	7	3	11	3	..	3	6	12	82
F_2 generation		F_3 generation											
Corinthian purple	1	3	..	1	..	..	..	..	..	..	..	..	4
	1	..	..	..	..	4	..	..	3	5	..	1	13
Hay's russet	1	1	..	..	..	..	1	..	..	..	..	..	2
	1	..	..	..	..	..	..	2	13	2	..	3	20
	1	..	..	..	..	..	18	5	9	1	..	12	45
	2	..	..	..	..	..	12	..	3	1	..	2	18
	1	..	..	..	..	..	17	..	..	..	..	12	29
	1	..	..	..	..	..	11	..	..	..	..	..	11
Deep Corinthian red	1	..	..	..	..	..	..	6	..	..	..	2	8
Oxblood red	1	..	..	..	..	..	2	..	7	2	..	1	12
Vinaceous fawn	1	..	..	..	..	1	..	..	..	1	..	18	20
	5	..	..	..	..	..	..	..	..	..	..	27	27
Testaceous	4	..	..	..	..	..	..	..	..	..	..	53	53

very likely give different results from those obtained with other Red Kidney beans.

The F_1 of this cross was not mottled so that neither the *R* nor the *C* genes were segregating. This is rather disconcerting because the presence of *R* has been shown to be the reason for the oxblood red color in the China Red variety in crosses with other strains of Red Kidney. This cross was different in other respects as well. In the F_2 population of 82 plants, nine colors were recognized: Corinthian purple (plate 2, fig. 46); liver brown (plate 2, fig. 47); chestnut-brown (plate 2, fig. 48); mahogany red; Hay's russet (plate 2, fig. 49) deep Corinthian red (plate 2, fig. 50); oxblood red (plate 2, fig. 51); vinaceous-fawn (plate 2, fig. 52); and testaceous (plate 2, fig. 53). The occurrence of liver brown and Corinthian purple indicates that *Bl* is segregating; similarly the brown segregates indicates the presence of some brown color modifiers. Oxblood red was reclaimed only three times in the population, hinting that its expression is due to a double recessive condition of two genes; the number expected for a 15:1 ratio in a population of 82 is 5.1. Only one oxblood red was tested in F_3. This one did not breed true as expected on the above hypothesis. It segregated 1 Hay's russet and 1 testaceous in a population of 12.

The vinaceous-fawn color was proved to be a variation of testaceous because F_3 progenies from this color all bred true for testaceous except one which had 1 oxblood red and 1 mahogany red plant in a population of 20. This could be explained as a natural outcross in the F_2 generation. The vinaceous-fawn and testaceous colors, then, can be combined in F_2, giving a total of 18 plants. This is about one-fourth of the population. The number expected on a 3:1 ratio is 20.5; this fits the expected ratio with a probability value of 0.53.

Hay's russet showed in the F_3 tests that it may segregate both oxblood red and testaceous colors. It, therefore, carries brown modifiers which are able to alter the colors in red beans.

It is interesting to note that seven of the ten F_3 progeny rows tested, segregated testaceous. The number of testaceous plants segregated in these seven progenies was 33 in a total population of 145. When these data are fitted to a 3:1 ratio the probability value is 0.54.

DARK RED KIDNEY × RED KIDNEY

(Formula: *P R Rk Bl* × *P r rk bl*)

This cross segregated like the crosses involving China Red. Dark Red Kidney is reddish purple classed as Indian purple (plate 1, fig. 4). It should therefore carry *Bl*. Since this cross segregated purple and red

TABLE 15

DARK RED KIDNEY × RED KIDNEY, CROSS NO. 34.167

(Formula: $P\ R\ Rk\ Bl \times P\ r\ rk\ bl$)*

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Purple/buff $(\frac{R}{r}\ Rk\ Bl)$	Purple/testaceous $(\frac{R}{r}\ rk\ Bl)$	Red/buff $(\frac{R}{r}\ Rk\ bl)$	Red/testaceous $(\frac{R}{r}\ rk\ bl)$	Indian purple $(R\ Bl)$	Oxblood red $(R\ bl)$	Buff $(r\ Rk)$	Testaceous $(r\ rk)$	Total	Probability values
F_1 generation				**F_2 generation**									
Purple/buff: Raisin black/avellaneous	$\frac{R}{r}\ \frac{Rk}{rk}\ \frac{Bl}{bl}$	18:6:6:2:12:4:12:4	12	113	41	60	0	111	24	86	23	458	Low†
F_2 generation				**F_3 generation**									
Purple/buff: Dark perilla purple/avellaneous	$\frac{R}{r}\ \frac{Rk}{rk}\ \frac{Bl}{bl}$	18:6:6:2:12:4:12:4	10	29	6	9	4	28	4	18	13	111	0.10
Dark perilla purple/avellaneous	$\frac{R}{r}\ Rk\ \frac{Bl}{bl}$	6:0:2:0:3:1:4:0	3	9	..	5	..	6	1	2	..	23	0.45
Dark perilla purple/avellaneous	$\frac{R}{r}\ \frac{Rk}{rk}\ Bl$	6:2:0:0:4:0:3:1	2	2	4	..	..	2	..	2	2	12	0.10
Dark perilla purple/avellaneous	$\frac{R}{r}\ Rk\ Bl$	2:0:0:0:1:0:1:0	4	12	..	..	..	8	..	4	..	24	0.50
Purple/testaceous: Raisin black/Corinthian red	$\frac{R}{r}\ rk\ \frac{Bl}{bl}$	0:6:0:2:3:1:0:4	7	..	28	..	9	13	8	..	12	70	0.30
Raisin black/Co-	R [illegible]	0:2:0:0:1:0:0:1	8	..	42	..	..	26	..	..	26	94	0.60

Red/buff:													
Bordeaux/light pinkish cinnamon..	$\frac{R}{r}\frac{Rk}{rk}\,bl$	0:0:6:2:0:4:3:1	1	..	..	3	0	..	3	3	1	10	0.73
Oxblood red/light pinkish cinnamon..	$\frac{R}{r}\frac{Rk}{rk}\,bl$	0:0:6:2:0:4:3:1	2	..	..	7	2	..	4	4	2	19	
Bordeaux/light pinkish cinnamon..	$\frac{R}{r}\,Rk\,bl$	0:0:2:0:0:1:1:0	4	..	..	15	..	..	9	5	..	29	0.98
Oxblood red/light pinkish cinnamon..	$\frac{R}{r}\,Rk\,bl$	0:0:2:0:0:1:1:0	5	..	..	22	..	..	10	12	..	44	
Red/testaceous:													
Bordeaux/light pinkish cinnamon..	$\frac{R}{r}\,rk\,bl$	0:0:0:2:0:1:0:1	1	..	..	..	4	..	2	..	2	8	0.99
Indian purple:													
Raisin black........	$R\,\frac{Bl}{bl}$	0:0:0:0:3:1:0:0	5	..	..	..	..	46	11	..	..	57	0.40
Indian purple......	$R\,\frac{Bl}{bl}$	0:0:0:0:3:1:0:0	7	..	..	..	..	55	17	..	..	72	
Indian purple......	$R\,Bl$	0:0:0:0:all	3	..	..	..		29	..	..	..	29	...
Raisin black........	$R\,Bl$	0:0:0:0:all	10	..	..	..	..	91	..	..	..	91	...
Oxblood red:													
Victoria lake........	$R\,bl$	0:0:0:0:0:all	10	..	..	..	..	..	74		..	74	..

* All genotypes in the table are homozygous for *P*.

† The word "low" is used in those cases where the probability value is less than 0.01.

self-colored beans it must be assumed that *bl* came from Red Kidney. The segregation of *Bl* is somewhat surprising because in all other crosses involving Red Kidney *Bl* is present. The results of this cross are summarized in table 15. In F_2 purple/buff was described as raisin black/avellaneous and in F_3 as raisin black/light pinkish cinnamon (plate 1, fig. 26). The purple/testaceous class was described as raisin black/Corinthian red in F_2 and as Indian purple/testaceous in F_3 (plate 1, fig. 13). The red/buff phenotype was divided into Bordeaux/light pinkish cinnamon and oxblood red/light pinkish cinnamon; in F_3 they were all described as oxblood red/light pinkish cinnamon (plate 1, fig. 21). No red/testaceous beans were recognized in the F_2; in F_3, they were labeled oxblood red/testaceous (plate 1, fig. 27). The purple phenotype included raisin black and Indian purple in F_2, dull violet-black (plate 1, fig. 23), and Indian purple (plate 1, fig. 29). The red beans were described as Victoria lake in F_2 and as oxblood red (plate 1, fig. 25) in F_3. Buff was called light pinkish cinnamon in F_2 and pinkish cinnamon (plate 1, fig. 7) in F_3. The testaceous (plate 1, fig. 1) phenotype was called by that color name in both F_2 and F_3 generations.

The F_2 population of 458 plants gave a poor fit for the expected ratio. This was because of the fact that one phenotype, red/testaceous, was not recognized. This was clearly an error in classification because one of the thirteen red/buff F_2 plants subjected to F_3 progeny test proved to be a red/testaceous genotype. In the purple/buff F_2 plants grown in F_3 ten segregated for *R*, *Rk*, and *Bl*; three for *R* and *Bl*; two for *R* and *Rk*; and four for *R* only. Fifteen purple/testaceous F_2 plants were tested. Seven segregated for *R* and *Bl*, and eight for *R* only. Twelve red/buff plants were grown in F_3. Three segregated for *R* and *Rk* and nine for *R* only. The single red/testaceous plant tested in F_3 was classed as a red/buff in F_2; it segregated for *R*.

In the purple phenotypes two shades of purple were distinguished in F_2, raisin black and Indian purple. In breeding behavior these were identical. Five raisin black F_3 progenies segregated for *Bl* and ten bred true; seven Indian purple progenies segregated for *Bl* and three bred true. The oxblood red group was called Victoria lake in F_2; however, in F_3 ten progenies bred true for oxblood red. No buff or testaceous F_2 plants were grown in F_3.

LONG ROMAN × CHINA RED, AND RECIPROCAL

(Formulas: *P M R Rk bl* × *P m R Rk bl* and *P m R Rk bl* × *P M R Rk bl*)

In the cross, Red Kidney × Long Roman (table 3) the red/buff Long Roman (plate 1, fig. 3) was found to be of the genetic constitution *P M*

TABLE 16

LONG ROMAN × CHINA RED (CROSS NO. 33.063) AND RECIPROCAL (CROSS NO. 33.070)
(Formulas: *P M R Rk bl* × *P m R Rk bl* and *P m R Rk bl* × *P M R Rk bl*)*

Parental colors	Parental genotypes	Expected ratios in progenies	Progenies tested	Segregants: Red/buff (*M R Rk bl*)	Segregants: Oxblood red (*m R Rk bl*)	Segregants: Total	Probability values
F_1 generation				*F_2 generation*			
l/buff: ordeaux/pale pinkish buff, cross no. 33.063	$\frac{M}{m}$ *R Rk bl*	3:1	3	132	54	186	0.20
ordeaux/pale pinkish buff, cross no. 33.070	$\frac{M}{m}$ *R Rk bl*	3:1	3	100	34	134	0.90
Total	$\frac{M}{m}$ *R Rk bl*	3:1	6	232	88	320	0.30
F_2 generation				*F_3 generation*			
l/buff: ordeaux/pale pinkish cinnamon	$\frac{M}{m}$ *R Rk bl*	3:1	1	7	1	8	0.43
maranth purple/pale pinkish cinnamon	*M R Rk bl*	all:0	1	17		17	...
lood red: ordeaux	*m R Rk bl*	0:all	2		68	68	
ompeian red	*m R Rk bl*	0:all	1		15	15	

* All genotypes in the table are homozygous for *P*.

Rk bl. The China Red has been found to be *P R Rk bl* (table 12) and *P R rk bl* (table 13). Since genes for two types of mottling, *Rr* and *M*, have been shown in these two varieties it was hoped that an interaction of the two could be seen in this cross. In that case the F_1 should show double mottling and the F_2 should segregate into 6 double mottled *Rr M*: 2 mottled *Rr* : 6 mottled *M* : 2 self-colored *r m* and *R m*.

However, in this reciprocal cross shown in table 16, the F_1 was red/buff and in F_2 there was segregation for mottled and self-colored oxblood red in the ratio of 3:1, with a probability value of 0.30, for a population of 320. On the basis of a 3:1 ratio there should be 80 reds. There were actually 88 so that a 14:2 ratio is very improbable.

As expected, there is no segregation for *Bl* since both varieties have been shown to be homozygous for *bl*.

In the F_2, four colors were recognized: the red/buff phenotype was classified as Bordeaux/pale pinkish cinnamon and amaranth purple/pale pinkish cinnamon; and the red phenotype was divided into Bordeaux and Pompeian red. In the F_3 progeny tests there was overlapping of the colors so that in table 16 they are grouped in only two classes, red/buff and red.

Only four F_2 plants were grown in F_3. One red/buff segregated for *M* and one bred true. Both oxblood reds bred true.

Since no testaceous phenotypes arose in this cross both varieties must have been homozygous for *Rk*; and since no purple plants were found they were both homozygous for *bl*. The genotype of the China Red may then be written, *P m R Rk bl*; and for Long Roman, *P M R Rk bl*. The presence of *R* in Long Roman, however, was not detected in crosses with Red Kidney (table 3). The poor fit to expectation in the crosses reported there, however, was due to misfits of two mottled classes red/buff and red/testaceous. Segregation for *M* was 256 mottled : 78 self-colored; expected, 250.5:83.5. Had *R* been segregating simultaneously, the ratio of mottled to self-colored should have been 292.25:41.75. It seems probable that the red mottling is due to the interaction of *M* and *R*. To explain all the facts presented here *M* and *R* would have to be linked. Such a linkage of *M* and *R* offers a workable hypothesis as to the nature of the red in red-mottled beans. In the previous crosses the cause of the red mottling was not discussed; *M* was considered to be a gene which restricts the expression of the darker color in bicolored beans, and it has been shown to be independent of *Rk* and *Bl*. If *M* and *R* were linked, the following color types would be expected: purple/buff would be *P MR Rk Bl* or $P \frac{mR}{mr}$ *Rk Bl*; purple/testaceous, *P MR rk Bl* or $P \frac{mR}{mr}$ *rk Bl*;

red/buff, $P\ MR\ Rk\ bl$ or $P\ \frac{mR}{mr}\ Rk\ bl$; red/testaceous, $P\ MR\ rk\ bl$ or $P\ \frac{mR}{mr}\ rk\ bl$; purple, $P\ mR\ Rk\ Bl$ or $P\ mR\ rk\ Bl$; oxblood red, $P\ mR\ Rk\ bl$ or $P\ mR\ rk\ bl$. Thus the oxblood red color in both self-colored and red-mottled beans could be due to the same gene, *R*. If there is a linkage between *M* and *R* it must be very strong because no cross-overs have been noted. The crosses reported in tables 1, 2, and 3 are between red/buff mottled beans and Red Kidney. Assuming linkage, these crosses may be represented as $P\ MR\ Rk\ bl \times P\ mr\ rk\ Bl$; the F_1 would be $\frac{P}{P}\ \frac{MR}{mr}\ \frac{Rk}{rk}\ \frac{bl}{Bl}$. The cross-over classes would be *mR* and *Mr*; of these, the *mR* cross-overs should be easily identified as self-colored oxblood red, $P\ mR\ bl$, or self-colored purple, $P\ mR\ Bl$. Since none of these appeared in any of these crosses, the crossing-over would have to be very small, if any. This argument is faulty for the same reason that Emerson's (*3*) *YZ* mottling theory was. Tjebbes (*24*) found close linkage between a red gene *R* and a striping gene *S* which occurs in the Cranberry variety. His red gene is not the same as the one encountered here because when heterozygous it does not produce mottling. It is probable, also, that *M* and *S* are not identical. It seems to be a strange coincidence that two red genes should each be linked with a mottling gene. More critical data are needed to study the interaction of *M* and *R*.

CHINA RED × MEXICAN RED, AND RECIPROCAL

Both these varieties are dark red, matching Ridgway's (*18*) oxblood red very closely. Mexican Red, however, has a black hilum ring. The F_1 was slightly darker than either parent and was classed as Victoria lake although it was more purple than this color. The hilum ring was black. In F_2, 52 mottled beans were found in a population of 364. These mottled ones were not recognized until some mottled beans appeared in F_3. The remnant F_2 seed was then reëxamined and the F_2 results given in table 17 are based on the second examination. It is possible therefore that some F_2 seed which were grown in F_3, although described as self-colored, were actually mottled. Unfortunately no remnant seed was available for those F_2 plants submitted to progeny tests. As is indicated in table 17 some mottled beans appeared in F_3 from all three colors tested. From Victoria lake, two progenies out of eighteen tested segregated 5 mottled and 26 self-colored; from oxblood red three progenies out of twenty-five segregated 11 mottled and 37 self-colored; and from Vandyke red five progenies out of twenty-seven tested segregated 25

TABLE 17

SEGREGATION FOR SEED-COAT COLOR IN CHINA RED × MEXICAN RED (CROSS NO. 34.172) AND RECIPROCAL (CROSS NO. 34.176)

Parental colors	Parental color of hilum ring	Progenies tested	Segregants								
			Victoria lake/testaceous	Oxblood red/testaceous	Pompeian red/testaceous	Victoria lake	Perilla purple	Oxblood red	Pompeian red	Ocher red	Total
F_1 generation			*F_2 generation*								
Victoria lake:											
Cross no. 34.172	Black	10	..	4	28	29	3	93	82	15	254
Cross no. 34.176	Black	6	1	14	5	15	8	39	21	7	110
Total	Black	16	1	18	33	44	11	132	103	22	364
F_2 generation			F_3 generation								
Victoria lake	Black	1	4	..	..	12	..	2	..	..	18
		1	..	..	..	7	1	5	..	..	13
		1	..	..	..	2	..	4	3	..	9
		8	..	..	..	63	..	35	..	..	98
		4	..	..	..	36	..	..	..	..	36
Victoria lake	No hilum ring	1	..	1	..	2	..	5	5	..	13
		1	..	..	..	4	..	4	..	..	8
		1	..	..	..	5	..	..	..	1	6
Oxblood red	Black	2	..	10	..	..	..	26	1	..	37
		1	..	..	..	4	2	9	2	..	17
		2	..	..	..	8	..	14	3	..	25
		1	..	..	..	..	..	13	1	..	14
		7	..	..	..	..	..	74	..	..	74

Oxblood red...........	No hilum ring	1	..	1	..	2	1	5	2	..	11
		2	..	..	..	3	.	17	3	3	26
		3	..	..	..	.	..	23	8	6	37
		5	..	..	..	.	.	31	7	..	38
		1	..	..	..	.	.	11	..	..	11
Vandyke red...........	Black.........	1	..	8	..	2	..	5	4	..	19
		1	..	..	..	2	.	5	3	..	10
		1	..	3	..	..	.	2	3	..	8
		2	..	10	..	..	.	26	8	..	44
		2	..	1	3	..	.	10	10	3	27
		1	..	..	..	.	..	4	4	..	8
		1	..	..	..	.	.	9	.	..	9
		1	..	..	.	.	.		..	11	11
Vandyke red...........	Orange........	5	..	..	..	.	.	33	18	..	51
		2	..	..	..	..	..	.	7	22	29
		2	..	..	.					10	10
Vandyke red...........	No hilum ring	4	..	..	..			13	22	7	42
		2	..	..	..	.	.	19	7		26
		1	..	..	.			12		1	13
		1	..	..			.	..	3	1	4

mottled and 73 self-colored. It is thus apparent the segregation of mottled and self-colored beans in this hybrid is not constant. If the mottling were due to the action of the *R* gene, the self-colored beans should breed true unless some modifying factors prevented the expression of mottling. The mottled types should segregate mottled and self-colored plants in the ratio of 1:1.

The only available data on this question are the results from progeny tests of two F_3 mottled plants. These segregated 10 mottled and 11 self-colored. This information though meager bears out the assumption that the reactions of the *R* gene were obscured in F_1 and partially in F_2 by modifying genes and it was not until these were eliminated in F_3 that clear-cut segregation for *R* could be detected.

The segregation of color of the seed coat in this cross is almost as baffling. The shades of red obtained in the F_2 and F_3 were so numerous and gradual that separation into modal classes was difficult. It is certain, however, that no testaceous beans were obtained in any of the F_2 or F_3 populations. Since China Red has been shown to carry *Rk* (table 12) and *rk* (table 13), and since no testaceous *rk* types appeared in this cross, both parents must have been homozygous for the *Rk* gene. It must be assumed, however, that the presence of other modifying genes prevented the buff *Rk* types from appearing because no buff beans were found in any of the offspring from this cross.

The presence of a colored hilum ring is a difficult character to study because not all beans from a single plant show the hilum ring color. It is therefore very easy to make errors in classification. Furthermore, the color of the hilum ring depends largely on the color of the seed coat. This is demonstrated in the F_2 data. The beans were classed as Victoria lake, perilla purple, oxblood red, Pompeian red, and ocher red. There were 44 plants with Victoria lake seed-coat color, 36 with black hilum ring, 1 with orange ring, and 7 with no ring. All 11 of the plants with perilla purple seed coats had black hilum ring. The oxblood red plants numbered 132 of which 89 had black ring, 15 had orange, and 28 had no ring. The 132 Pompeian red plants were classed as 72 with black hilum ring, 18 with orange, and 13 with no ring. In 22 ocher-red plants, 11 had black hilum ring, and 11 had orange. Segregation for hilum-ring character in this cross is shown in table 18. Some progenies bred true for both black and orange hilum ring but no true-breeding progenies with no hilum ring were obtained. Some of the F_2 plants classed as having no hilum ring proved in progeny tests to have rings. The character for orange hilum ring bred true in two progenies of oxblood red and two of Vandyke red. Black ring seems to be dominant over orange but there

are cases of F_2 plants with orange ring segregating plants with black rings. The genetic nature of the hilum ring character therefore is difficult to understand.

TABLE 18

SEGREGATION FOR HILUM-RING COLOR IN CHINA RED × MEXICAN RED (CROSS NO. 34.172) AND RECIPROCAL (CROSS NO. 34.176)

Parental color	Parental color of hilum ring	Progenies tested	Hilum-ring color of segregants			Total segregants
			Black	Orange	No hilum ring	
F_1 generation			F_2 generation			
Victoria lake	Black	16	269	47	48	364
F_2 generation			F_3 generation			
Victoria lake	Black	7	59	..	31	90
		1	5	4	..	9
		7	75	..	..	75
Victoria lake	No ring	2	4	11	4	19
		1	3	..	5	8
Oxblood red	Black	4	39	15	10	64
		3	31	..	3	34
		1	..	10	7	17
		5	52	..	..	52
Oxblood red	No ring	6	9	28	37	74
		4	.	23	6	29
		2	.	20	..	20
Vandyke red	Black	5	60	13	17	90
		3	15	6	..	21
		2	14	..	3	17
		1	8	..	..	8
Vandyke red	Orange	5	6	42	3	51
		4	..	39	..	39
Vandyke red	No ring	6	21	42	5	68
		2	..	17	..	17

MEXICAN RED × RED KIDNEY

The results from this cross are summarized in table 19. The F_1 was violet carmine. The names given to the color classes varied somewhat between the F_2 and F_3 generations. The relation between them was as follows: Beans which were *classified as dull purplish black in* F_2 were black and Indian purple in F_3; Victoria lake was used in both generations; in F_2

TABLE 19

Mexican Red × Red Kidney, Cross No. 33.496

Parental color	Progenies tested	Segregants: Black	Indian purple	Victoria lake	Chocolate	Oxblood red	Vandyke red	*Testaceous*	Total
F_1 generation		F_2 generation							
Violet carmine	20	..	14	254	14	62	34	118	496
F_2 generation		F_3 generation							
Dull purplish black	1	5	4	..	..	1	..	1	11
	1	1	1	2	..	2	..	..	6
	1	3	7	..	3	1	..	..	14
	1	1	3	..	..	1	..	..	5
	1	1	2	3	..	..	..	..	6
	1	2	1	..	..	..	..	..	3
	1	3	..	..	..	..	..	..	3
	1	..	1	1	1	..	..	..	3
	2	..	4	..	4	..	..	..	8
	2	..	3	..	..	..	..	..	3
Liver brown	1	..	1	3	1	..	..	1	6
	1	..	2	..	..	..	..	1	3
	1	..	2	..	1	1	..	..	4
	2	..	7	..	..	2	..	..	9
	1	..	1	1	1	..	..	..	3
	1	..	1	..	..	..	..	..	1
	1	..	..	..	..	..	..	1	1
	2	..	..	2	..	7	3	..	12

Oxblood red	2	..	..	..	..	6	4	2	12
	2	..	..	..	..	3	5	..	8
	3	..		..	..	15	..	.	15
Mars brown	1	.		..	1	1	1	1	4
	1	..		..	3	..	..	3	6
	1	..	.	..	3	.	1	1	5
	1	..	..	..	1	..	.	..	1
	1	..	..	..	..	2	..	..	2
	1	..	..	..	..	..	..	3	3
Orange cinnamon	10	..	..	..	..	..	.	53	53
Ferruginous	6	..	..	..	..	..	..	28	28

liver brown and burnt umber were grouped together as chocolate in F_3; oxblood red was used in both generations; beans classed as Pompeian red in F_2 were called Vandyke red in F_3. A number of light-red types similar to testaceous were distinguished in F_2 but all proved to be testaceous when submitted to progeny tests. These F_2 color names, then, can all be grouped together: orange-cinnamon, Japan rose, ferruginous, and testaceous. F_3 progeny tests were made of a number of F_2 plants but owing to poor stand in the nursery, the F_3 populations were too small to obtain accurate ratios.

Although the colors do not segregate in definable ratios a number of illuminating facts are observed. The colors obtained in this cross are illustrated in plate 2, figures 54–59. The F_1 was purplish red (violet carmine) therefore the *Bl* gene was able to modify the color in this hybrid. It appears that each parent contributed some purple modifying genes because in F_3 progenies from F_2 Indian-purple plants (plate 2, figs. 63–64), some beans appeared which could be described by no better word than black (plate 2, fig. 54). These may well be due to accumulation of darkening modifiers contributed from both parents. The light-red beans, such as Vandyke red (plate 2, fig. 58), may well be due to homozygous combinations of red genes with *bl* and other recessive purple modifiers.

Another interesting fact noted in this cross is the absence of segregation of color of the hilum ring, presumably due to the fact that both Red Kidney and Mexican Red have colored hilum rings; the ring in the former is orange and in the latter, black. On this basis, crosses between Red Kidney and China Red or Dark Red Kidney should have segregated for colored hilum ring. This, however, was not observed; but no special attention was paid to this character in those crosses.

Still another fact is apparent in the Mexican Red × Red Kidney cross. In the F_2 population of 496 plants, there were 118 testaceous plants (table 19). Fitted to a 3:1 ratio there should have been 124; the probability value for such a fit is 0.54. In the F_3 progenies there were 7 which segregated 10 testaceous plants in a population of 47. The probability value for these results, fitting a 3:1 ratio, is 0.57. Thus it is apparent that the recessive gene *rk* is segregating normally in this cross. But what has become of *Rk* since no buff beans were found in any of the progenies? It is now apparent that Mexican Red either has a third allelomorph of the *Rk rk* gene pair or other color genes prevent its expression as buff.

Still another fact is apparent in this cross which should not be overlooked and that is the absence of mottled beans. Since some mottled beans were obtained in the China Red × Mexican Red cross the assump-

tion was made that the *R* gene was segregating. China Red is known to carry the dominant allelomorph *R*; so, if mottling were due to heterozygous *R*, Mexican Red must carry *r*. This fits in with the facts obtained in this cross. Red Kidney has been shown to carry *r* and if Mexican Red does also, no mottled beans are expected in the progeny of this cross.

MEXICAN RED × DARK RED KIDNEY

The F_1 of this cross was classed as Vandyke red with a black hilum ring. In F_2 it segregated for the hilum-ring character. The results of the segregation for seed-coat color are given in table 20 and for the hilum ring character in table 21.

Regarding mottling, much the same result was obtained here as in the China Red × Mexican Red cross. The faint mottling was entirely overlooked in F_2. When the F_3 was obtained showing mottled beans, the F_2 remnants were reëxamined and four mottled beans were found which had been previously classified as Corinthian purple. Two F_2 progenies segregated such a high proportion of mottled offspring in F_3 that they must have been mottled in F_2. These two progenies, which are indicated in table 20, consisted of 42 plants of which 22 were mottled. For a 1:1 ratio there should have been 21. Fitted to such a ratio the probability value is 0.76. It is apparent that the *R* gene is segregating in this cross but some modifying genes prevent the expression of mottling in some cases. Further proof for the presence of *R* was obtained by subjecting known mottled F_3 beans of this cross to progeny tests. From eight progenies 120 plants were harvested, 56 being mottled and 64 self-colored. These data fitted to a 1:1 ratio give a probability value of 0.47.

Since some reddish purple (Indian purple, plate 2, figs. 63, 64), and purple (perilla purple, plate 2, fig. 65) beans were obtained, it is assumed that the color genes in Dark Red Kidney (Indian purple, plate 1, fig. 4) were responsible. No blacks, however, were found in the F_3 so there was no accumulation of dark modifiers as in Mexican Red × Red Kidney. In the cross Dark Red Kidney × Red Kidney (table 15) evidence of segregation of *Bl* was obtained. Thus the *Bl* gene carried by Red Kidney is not the same gene as the purple modifier in Dark Red Kidney or black beans would have been obtained in the F_3 of the cross Mexican Red × Dark Red Kidney. Oxblood red was reclaimed often in the F_3 of this cross and so was a still lighter red, classed as acajou red (plate 2, figs. 69, 70). Acajou red is lighter in color than the Mexican Red parent and indicates that it may have fewer dominant color genes for red or purple than either parental variety. No testaceous beans were obtained in this cross indicating that neither parent carries *rk*.

TABLE 20

SEGREGATION FOR SEED-COAT COLOR IN MEXICAN RED × DARK RED KIDNEY, CROSS NO. 34.171

Parental colors	Parental color of hilum rings	Progenies tested	Segregants: Indian purple/Pompeian red	Segregants: Perilla purple/light perilla purple	Segregants: Oxblood red/Pompeian red	Segregants: Acajou red/testaceous	Segregants: Indian purple	Segregants: Perilla purple	Segregants: Oxblood red	Segregants: Acajou red	Total
F_1 generation			F_2 generation								
Vandyke red	Black	3	..	4	..	..	14	70	42		130
F_2 generation			F_3 generation								
Indian purple	Black	1*	..	..	3	..	3	..	2	2	10
		1	3	..	4	..	44		18	1	70
		3	..	..	4	..	45		26		75
		2		..	..		24		18		42
Corinthian purple	Black	1*	1	18	..	..	2	10	1	..	32
		1	1	..			9	8	5	1	24
		6	..	26	3	1	28	50	20	11	139
		5	..	9	..		11	59	11		90
		1	..	1	..	..	..	24		..	25
		4	..	..	..	..	17	21	7	..	45
		1		..	..	..		25			25
Deep hellebore red	Black	2	..	12	..	..	4	49	17	3	85
		1	..	1	..	..		20			21
		1	..	..	..	..	1	12	3	1	17
		2	..	..	..	..	..	32	..		32

Oxblood red	Black	1	..	..	1	..	..		33	1	35
		2	..	..	..	..	..	..	31	15	46
Deep hellebore red	Orange	2	..	3	..	..	..	15	6	..	24
		1	..	7	..	..	..	15	..	..	22
		1	..	..	..	..	..	6	15	8	29
		1	..	..	..	..	..	10	..	7	17
Oxblood red	Orange	2	..	..	..	..	..	2	40	20	62
		7	..	..	..	..	..	..	61	27	88
		1	..	..	..	..	.	.	3	..	3
Indian purple	No ring	2	..	..	..	.	..	.	9	7	16
Corinthian purple	No ring	1	..	..	..	..	7	29	3	..	39
Oxblood red	No ring	1	..	..	..	..	1	..	4	2	7
		2†	..	.	..	..	12	.	4		16
		1	..	.	..	..	..	3	9	..	12
		1	..	..	..	..	.		8	5	13
		4	..	..	..		..		43	.	43

* An F_2 plant, probably mottled.
† An F_2 plant, probably Indian purple.

In the study of the hilum-ring character, summarized in table 21, the same difficulties of clearly distinguishing the different phenotypes were encountered as described in the China Red × Mexican Red. Here there was further evidence that the color of the hilum ring and the color of the seed coat are associated. This condition has already been noted in the literature (*12, 17*). In the F_2 generation the Indian-purple progeny

TABLE 21

SEGREGATION FOR HILUM-RING COLOR IN MEXICAN RED × DARK RED KIDNEY, CROSS NO. 34.171

Parental color	Parental color of hilum ring	Progenies tested	Hilum-ring color of segregants: Black	Orange	No hilum ring	Total segregants
F_1 generation			*F_2 generation*			
Vandyke red	Black	3	82	20	28	130
F_2 generation			F_3 generation			
Indian purple	Black	7	93	39	65	197
Corinthian purple	Black	9	122	42	33	197
		8	114	31	..	145
		1	11	..	2	13
		1	25	..	..	25
Deep hellebore red	Black	2	54	26	5	85
		3	35	14	..	49
		1	21	..	..	21
Oxblood red	Black	3	53	16	12	81
Deep hellebore red	Orange	2	..	47	4	51
		3	..	41	..	41
Oxblood red	Orange	2	7	45	8	60
		1	1	2	..	3
		3	..	37	12	49
		4	..	41	..	41
Indian purple	No hilum ring	1	..	..	1	1
		1	..	1	14	15
Corinthian purple	No hilum ring	1	9	16	14	39
Oxblood red	No hilum ring	1	2	2	8	12
		4	..	17	21	38
		2	..	14	..	14
		2	..	..	27	27

were classed as 10 with black hilum ring and 4 with no ring; in the perilla purple, 59 had black hilum ring, 9 had orange, and 1 no ring; in the oxblood red, 9 had black hilum ring, 11 had orange, and 22 no ring; in the perilla purple/light perilla purple all 4 had black hilum rings.

The plants with black hilum rings seem to be able to segregate both orange rings and no rings as well as breed true. Orange hilum ring usually breeds true or segregates no ring but occasionally some progeny with black ring come from F_2 plants with orange hilum ring. F_2 plants classed as having no rings did not always breed true—in fact most of them reverted to orange rings or in a few cases black. Two F_2 progenies from oxblood with no hilum ring bred true in F_3.

As can be seen in table 20 there is some discrepancy in the color description of F_2 and F_3. The two colors, Corinthian purple and deep hellebore red recognized in F_2 were grouped together in F_3 as perilla purple.

NATURE OF THE COLOR COMPLEX IN MEXICAN RED

In the three crosses just discussed no attempt was made to give the genetic formula of Mexican Red. We can, however, make some assumptions which are based on the results of the crosses involving this variety.

Both China Red and Dark Red Kidney carry *R* and since some mottled beans were found in F_2 and F_3, when these varieties were used in crosses with Mexican Red, the mottling was attributed to the action of *R*. F_4 data from both China Red × Mexican Red and Mexican Red × Dark Red Kidney crosses were presented to show that mottled hybrid beans do segregate in the ratio of 1 mottled to 1 self-colored as expected. This was explained on the basis that the reactions of *R* were obscured by interactions of other color genes but when these modifiers were eliminated in the F_3 the action of *R* could be readily seen. Thus Mexican Red carries *r*. Since Red Kidney also carries *r* there should be no mottling in the progeny of a cross between these varieties. Since none were found this is further evidence that Mexican Red must carry *r*.

Some F_2 beans were obtained in these crosses which were darker than either parent, a fact explained by assuming that the Mexican Red carries purple modifiers as well as the other varieties and the dark colors are due to accumulation of these modifiers in homozygous condition in some genotypes. The reverse situation was also observed. Some F_2 beans were lighter red than either parent indicating the elimination of the dominant purple modifiers. The genetic nature of the colored hilum ring has not been settled in this work. Because it is difficult to always distin-

guish this character, errors are easily made in classification. After they have been made it is hard to reconcile the notes on the hybrids in the succeeding generation. There is some evidence that the color of the ring is associated with the color of the seed coat but there are also enough exceptions to make a general rule untenable.

Mexican Red was shown in crosses with Red Kidney to carry a dominant allelomorph of *rk* since one-fourth of the F_2 and segregating F_3 progenies were testaceous. China Red and Dark Red Kidney have been shown to carry *Rk* a dominant allel of *rk* which makes beans buff in color in the absence of the dominant red gene *R*. Now, since Mexican Red does not carry *R*, and since no buff beans were found in any of the crosses, it must carry other red color genes which prevent *Rk* from appearing as buff. Another explanation, advanced earlier in the paper is that this variety may carry a third allel in the *Rk rk* series. No critical data are available to make a choice between these two possibilities.

Crosses involving Mexican Red were the most difficult to analyze genetically but the hybrids show more promise as a foundation for a breeding program to improve the color of Red Kidney than any other variety tested. The new light-red colors which may be useful are: Pompeian red (plate 2, fig. 44), and ocher red (plate 2, fig. 45) from the cross China Red × Mexican Red; Vandyke red (plate 2, fig. 58) from the cross Mexican Red × Red Kidney; and acajou red (plate 2, figs. 69, 70) from the cross Mexican Red × Dark Red Kidney. Whether these reds will prove useful to this end remains to be seen in later breeding work.

SUMMARY

Hybrids between red-seeded varieties of common beans were made to study the genetic nature of red. Ridgway's (*18*) color nomenclature was used in the descriptions. The results of this study are applicable in improvement of the Red Kidney variety, which changes in time from red to brown or tan while in storage or when in sunlight. Six genes were encountered which affect seed-coat color or its distribution.

P is a primary pigmentation factor necessary for any color to develop. Beans with *P* but without any complementary pigmentation color genes are white. All the bean varieties studied carried one or more complementary color factors. Beans homozygous for *p* are white regardless of the color genes they may have.

M is a mottling gene which was found in a number of red-mottled varieties; its recessive allelomorph, *m*, is self-colored.

Rk, a gene for buff color, is the dominant allelomorph of *rk*, which is responsible for the testaceous color typical of the Red Kidney variety.

The interactions of *Rk rk* have not been known heretofore. *M Rk* beans are mottled on buff background, and *M rk* are mottled on testaceous background.

R is a gene for deep red (oxblood red). In the genotypes studied *R Rk* and *R rk* were oxblood red; *r Rk*, buff; and *r rk*, testaceous. Beans heterozygous for *R* are mottled: those with *Rr Rk* are mottled on buff background and those with *Rr rk* are mottled on testaceous.

Bl is a color modifier which changes oxblood red to purple. It also changes red-mottled beans to purple-mottled when the mottling is caused by either heterozygous *R* or *M*.

E is the dominant allelomorph of *e*, a gene for eye pattern. *E* beans are self-colored. The eyed variety used was white with a red eye, the red being due to *rk*.

No linkage was found between *Rk M Bl*, *Rk R Bl*, or *Rk E*. Linkage between these genes and *P* could not be demonstrated because all *p* genotypes are white. Some data were obtained indicating complete linkage of *M* and *R*. No cross-over classes were found.

Not one of these genes was suitable as a color modifier of Red Kidney. However, F_3 segregates were obtained in crosses involving Mexican Red which were nearer the ideal type. Further experiments are necessary to ascertain the practical value of these reds. The genotype of Mexican Red was not obtained because it carries a number of modifiers which made classification difficult. No buff segregates were found in crosses involving Mexican Red, although about one-fourth of the F_2 population was testaceous in the cross Mexican Red × Red Kidney. Mexican Red either has modifiers which prevent the expression of buff or it carries a third allelomorph for the *Rk rk* gene pair.

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PLATES

PLATE 1

PARENTAL VARIETIES:

Fig. 1. Red Kidney 4370.
Fig. 2. Nagazura 4390.
Fig. 3. Long Roman 4521.
Fig. 4. Dark Red Kidney (65)31.
Fig. 5. Speckled Kidney 50(51)30.
Fig. 6. China Red 4414.
Fig. 7. Buff *P Rk*.
Fig. 8. Mexican Red 4437.

F_3 SEGREGANTS OF WHITE KIDNEY × NAGAZURA:

Fig. 9. Raisin black/pinkish buff (*P M Rk Bl*).
Fig. 10. Indian purple/pinkish buff (*P M Rk Bl*).
Fig. 11. Dark heliotrope slate/pinkish buff (*P M Rk Bl*).
Fig. 12. Raisin black/testaceous (*P M rk Bl*).
Fig. 13. Indian purple/testaceous (*P M rk Bl*).
Fig. 14. Maroon/pinkish buff (*P M Rk bl*).
Fig. 15. Oxblood red/pinkish buff (*P M Rk bl*).
Fig. 16. Deep hellebore red/pinkish buff (*P M Rk bl*).
Fig. 17. Maroon/testaceous (*P M rk bl*).
Fig. 18. Oxblood red/orange cinnamon (*P M rk bl*).

F_3 SEGREGANTS OF CHINA RED × RED KIDNEY:

Fig. 19. Raisin black/pinkish buff ($P \frac{R}{r} Rk\ Bl$).
Fig. 20. Raisin black/testaceous ($P \frac{R}{r} rk\ Bl$).
Fig. 21. Oxblood red/light pinkish cinnamon ($P \frac{R}{r} Rk\ bl$).
Fig. 22. Oxblood red/testaceous ($P \frac{R}{r} rk\ bl$).
Fig. 23. Dull violet black (*P R Bl*).
Fig. 24. Dull purplish black (*P R Bl*).
Fig. 25. Oxblood red (*P r bl*).

F_3 SEGREGANTS OF DARK RED KIDNEY × RED KIDNEY:

Fig. 26. Raisin black/light pinkish cinnamon ($P \frac{R}{r} Rk\ Bl$).
Fig. 27. Oxblood red/testaceous ($P \frac{R}{r} rk\ bl$).
Fig. 28. Black (*P R Bl*).
Fig. 29. Indian purple (*P R Bl*).
Fig. 30. Violet carmine (*P R Bl*).

F_3 SEGREGANTS OF CHINA RED × MEXICAN RED:

Fig. 31. Victoria lake/testaceous, with black hilum ring.
Fig. 32. Oxblood red/testaceous, with black hilum ring.

PARENTAL VARIETIES:

Fig. 33. White Kidney 4516.
Fig. 34. Red Eye 4387.

F_2 SEGREGANT OF RED EYE × BUFF:

Fig. 35. Buff eye.

(*All natural size.*)

PLATE 2.

F_3 Segregants of China Red × Mexican Red:

Fig. 36. Pompeian red testaceous.
Fig. 37. Victoria lake, with black hilum ring.
Fig. 38. Oxblood red, with orange hilum ring.
Fig. 39. Oxblood red, with no hilum ring.
Fig. 40. Pompeian red, with black hilum ring.
Fig. 41. Victoria lake, with no hilum ring.
Fig. 42. Perilla purple, with black hilum ring.
Fig. 43. Oxblood red, with black hilum ring.
Fig. 44. Pompeian red, with orange hilum ring.
Fig. 45. Ocher red, with orange hilum ring.

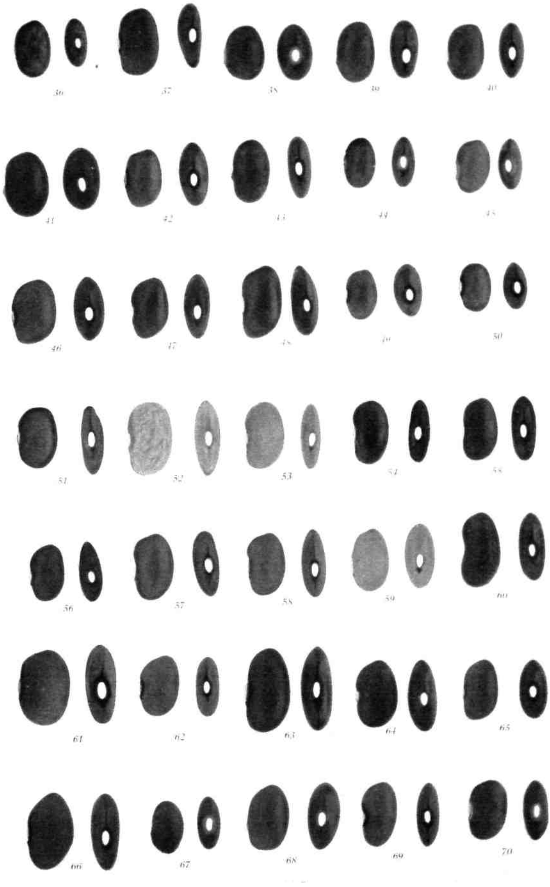
F_2 Segregants of China Red × Geneva Red Kidney:

Fig. 46. Corinthian purple.
Fig. 47. Liver brown.
Fig. 48. Chestnut brown.
Fig. 49. Hay's russet.
Fig. 50. Deep Corinthian red.
Fig. 51. Oxblood red.
Fig. 52. Vinaceous fawn.
Fig. 53. Testaceous.

F_3 Segregants of Mexican Red × Red Kidney:

Fig. 54. Black.
Fig. 55. Victoria lake.
Fig. 56. Chocolate.
Fig. 57. Oxblood red.
Fig. 58. Vandyke red.
Fig. 59. Testaceous.

F_3 Segregants of Mexican Red × Dark Red Kidney:

Fig. 60. Indian purple testaceous.
Fig. 61. Perilla purple light perilla purple.
Fig. 62. Oxblood red Pompeian red.
Fig. 63. Indian purple, with black hilum ring.
Fig. 64. Indian purple, with no hilum ring.
Fig. 65. Perilla purple, with black hilum ring.
Fig. 66. Oxblood red, with black hilum ring.
Fig. 67. Oxblood red, with orange hilum ring.
Fig. 68. Oxblood red, with no hilum ring.
Fig. 69. Acajou red, with black hilum ring.
Fig. 70. Acajou red, with orange hilum ring.

(All natural size.)